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BULLETIN OF THE TORREY BOTANICAL CLUB
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THE SHOOT OF BOTRYCHIUM INTERPRETED AS A SERIES OF DICHOTOMIES

M. A. CHRYSLER[1]

It has long been recognized that Ophioglossales exhibit a number of primitive features, especially in their sporangia, while they possess certain unusual features which distinguish them from Filicales, with which group there has been a persistent tendency to associate them. This was but natural on account of the fern-like sterile segment of the leaf in *Botrychium*. But the discovery of the Coenopteridales followed by that of Psilophytales has led to attempts to reinterpret the morphological features of Ophioglossales. This is notably true of Zimmermann's attempt to fit *Botrychium Lunaria* into his "Telomtheorie"; especially interesting is his hypothesis (1930, p. 203) that the fertile spike represents one branch of an ancient dichotomy in the plane perpendicular to that of the other divisions occurring in the leaf. Such a conjecture, if supported, would indicate a relation of the order to certain Coenopteridales and Rhyniaceae. This interpretation of the fertile spike was promptly taken up by Bower (1935), replacing the theories which he earlier entertained. Zimmermann's definition (1930, p. 65) of a telome (fertile or sterile) as an ultimate branch of a shoot, including its vascular bundle, constituting the morphological unit of the cormophyte shoot, was supplemented in 1938 by addition of the term *mesome* to express the idea of two or more telomes fused as they appear below a dichotomy. The two terms will in this paper be employed as thus defined. No attempt is here made to define a dichotomy in terms of development; the recent review by Sifton (1944) of the literature on the question as to what constitutes a dichotomy shows a notable lack of agreement among the workers in this field.

Since the presence of a vascular bundle characterizes a telome, the behavior of the bundles of the shoot in Ophioglossales should afford critical evidence as to the soundness of Zimmermann's interpretation of the fertile spike. He makes only slight reference to evidence from anatomy; it is the purpose of this study to investigate the evidence from this point of view. The genus *Botrychium*, generally regarded as the most primitive of the genera, has been found to be the most favorable for the purpose. The following species, named according to Clausen's memoir (1938), have been available:

Subgenus *Eubotrychium*.
B. boreale Milde: Sweden (herbarium material).
B. lanceolatum (Gmel.). Angstr., subsp. *angustisegmentum* (Pease & Moore) Clausen: Me., N. J., N. Y., Pa.

[1] Publication of the Bureau of Biological Research, Rutgers University.

[THE BULLETIN for September–October (72: 435–490) was issued September 5, 1945]

B. Lunaria (L.) Sw., var. *typicum:* Gaspé, Europe.
B. Lunaria, var. *minganense* (Victorin) Dole: Que. (herbarium material).
B. matricariaefolium A. Br., subsp. *typicum:* Me., N. J., N. Y., Pa., Gaspé.
B. pumicola Coville: Ore.
B. simplex Hitchc., var. *compositum* (Lasch) Milde: Cal.
B. simplex Hitchc., var. *tenebrosum* (A. A. Eaton) Clausen: Me., N. J., N. Y.
Subgenus *Sceptridium.*
B. dissectun Spreng. and var. *obliquum* (Muhl.) Clute: Me., N. H., N. J., Pa.
B. multifidum (Gmel.) Rupr., ssp. *typicum:* Pa., Gaspé.
B. multifidum, ssp. *silaifolium* (Presl) Clausen: N. H.
B. underwoodianum Maxon: Costa Rica (herbarium material).
Subgenus *Osmundopteris.*
B. lanuginosum (Wall.) Hk. & Grev.: Sumatra (herbarium material).
B. virginianum (L.) Sw.: N. J., Gaspé.

The object of securing material from widely separated localities was to be sure that climatic differences were not the cause of variations in anatomical structure. Plants differing considerably in size have been included. Material of *B. dissectum* and *multifidum* showing abnormalities such as extra fertile branches have also been examined. I am greatly indebted to the following sources of material: Professor R. T. Clausen, Mr. W. L. Dix, Mr. J. L. Edwards, Mr. G. G. Nearing, Brooklyn Botanic Garden, Gray Herbarium, Herbarium of University of California at Berkeley. In all cases the material was imbedded in paraffin and serial sections cut through the branching regions. One fortunate fact about members of this order is that the bud located at the base of the petiole of the present year's leaf contains an epitome of the leaf architecture, and requires the preparation of much fewer sections, although it has the disadvantage that the vascular tissues are still in a more or less immature stage.

OBSERVATIONS

What appears to be the primitive condition of the vascular system is best seen in members of the subgenus *Eubotrychium* (Milde) Clausen. All species of this group have been studied, and have been found to show a remarkable uniformity in their vascular plan; in fact individuals of one species may vary almost as much as do different species. *B. matricariaefolium* will first be considered. From the hollow central cylinder of the vertical rhizome arise a series of leaf traces which do not seem to show a definite phyllotaxy (see figure 25 representing *B. dissectum*); in some plants the distichous arrangement is approached. The bundle leaves the stele as a somewhat curved group of tracheids most of which are arranged in radial rows, as are the tracheids found in the stele; before the bundle reaches the region of the petiole, however, this "carry-over" of secondary structure disappears and the trace assumes the form of a collateral endarch bundle with a single protoxylem group (figs. 1, 5) which soon divides and at once the bundle splits into a right and a left half, each with a single protoxylem (figs. 2, 6). This doubling

of the trace usually occurs at the level where it emerges from the rhizome into the petiole, but may occur as much as 2 mm. above this level. In a strongly growing leaf the size of the trace may approach that of the remaining part of the stele (fig. 12), suggesting a dichotomous division of the vascular system. As the two petiolar strands rise each gradually rotates through nearly 90° so that their xylems face one another (fig. 3). Each bundle meanwhile increases considerably in size and assumes a curved form like a parenthesis (fig. 4), the protoxylem of each divides, and just below the level where fertile and sterile branches of the leaf separate, each bundle divides in the radial plane into two more or less equal parts (fig. 7), the size of each depending on the relative size of the two leaf-branches. This division is of course at right angles to the preceding division. Two bundles, one from each "parenthesis," diverge to the sterile branch, where they again undergo a rotation which brings their edges side by side and their xylems facing the fertile segment, i.e., adaxial (fig. 8); each bundle again divides into a right and a left portion, more or less unequally, and these divisions may occur at the same level or one ahead of the other; by a repetition of this process the vascular skeleton of the sterile branch is built up. Returning to the parenthesis, the two bundles which did not diverge run up into the sporogenous region of the fertile branch; they do not rotate through as great an angle as occurs in the sterile branch (figs. 8, 28), but at a higher level undergo fission, the lateral bundles supplying branches which eventually lead to sporangia, each with its bundle (fig. 28). It should be noted that the members of a pair of parentheses do not always divide at the same level, (fig. 9)—each behaves independently in this regard.

With respect to the other species in subgenus *Eubotrychium*, *B. Lunaria* can hardly if at all be distinguished from *B. matricariaefolium* by the vascular tissues. The same can be said of *B. boreale* and of *B. Lunaria* var. *minganense*. In *B. lanceolatum* the same general plan is present, but the parentheses undergo partial segregations (fig. 11) before the ab- and adaxial portions break off to supply the sterile and fertile branches respectively. The reason for this appears at once upon inspection of a plant; in this species the sterile and fertile branches typically divide very quickly after their separation; this feature is represented in the vascular structure by a precocious separation of the strands which lead to the various pinnae, etc. That is, there is an overlapping or telescoping of the dichotomies which were traced in the preceding paragraph. The result is that a pair of parentheses expands into what simulates a dictyostele; the units supplying the sterile branch, however, soon diverge and assume the form of a flattened row such as is characteristic of the plainly dorsiventral blade. *B. simplex*, especially the variety *tenebrosum*, in keeping with the slender form has smaller, more rounded bundles than occur in the larger species, but exactly the same series of

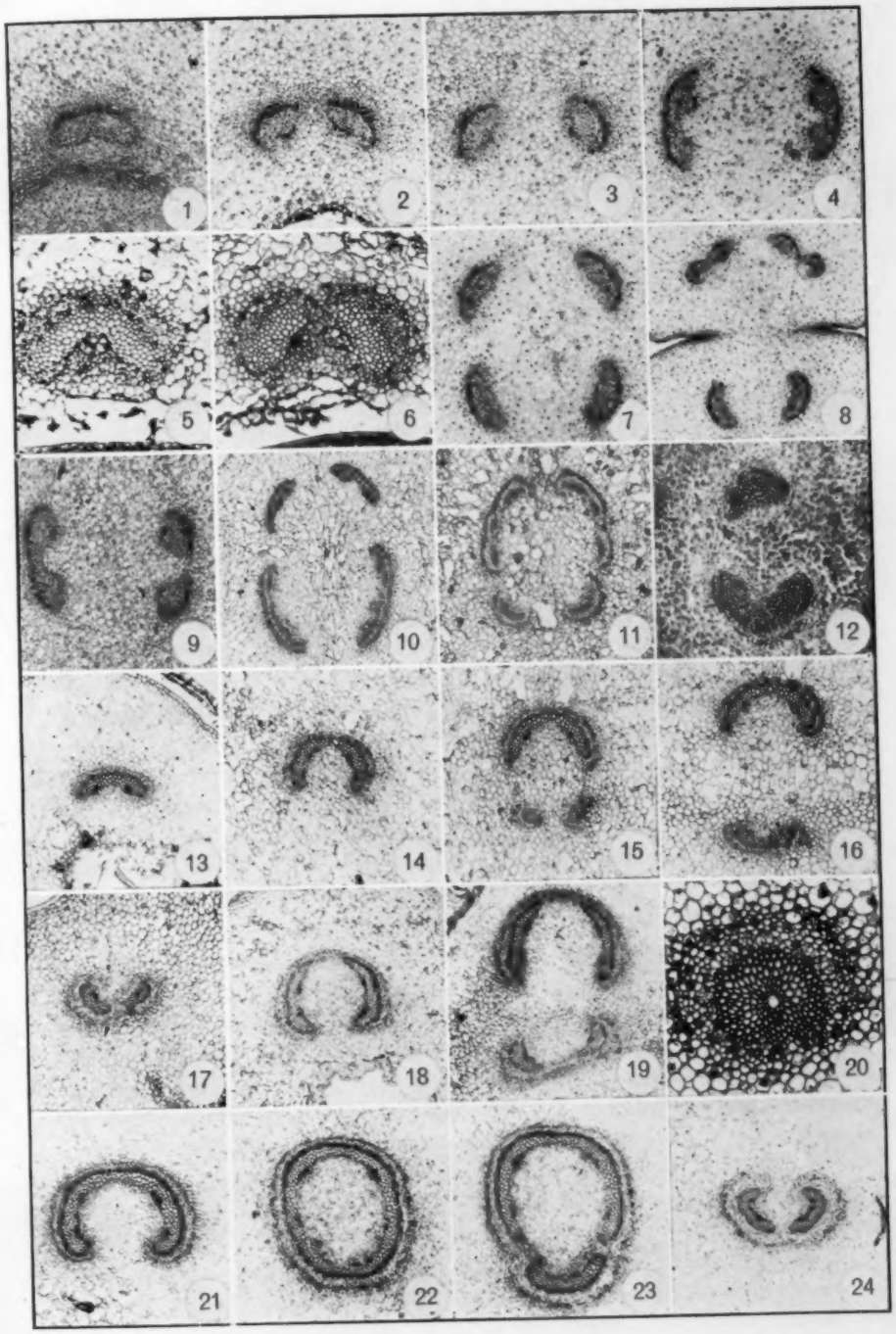
dichotomies of the petiolar trace are found. In *B. simplex* var. *compositum* the form and course of the bundles seem exactly the same as in *B. matricariaefolium*. The rare species *B. pumicola* (material from Dr. Clausen) presents one additional feature of interest. In the form and course of the bundles this species is similar to *B. simplex*, except that the two bundles belonging to the sterile branch divide before separation of the sterile from the fertile branch, i.e., lower than in the stage shown in figure 8. Hence six bundles (three pairs) traverse the common stalk for a distance of several millimeters. This condition is readily explained by the short stalk of the sterile branch (cf. *B. lanceolatum*).

In the subgenus *Sceptridium* Clausen (the group *Ternata* of Prantl) a different appearance is presented, and this is exhibited in all the species which have been available for study. *B. multifidum* is chosen to illustrate what may be regarded as the typical condition. The leaf-trace presents the same structure as in *Eubotrychium*, namely, it arises from the solenostele of the rhizome as a slightly curved bundle, at first with secondary xylem; later it is seen to possess a single protoxylem which at a slightly higher level divides (fig. 13). Unlike *B. matricariaefolium*, however, the trace remains undivided (except in rare cases, *vide infra*). As it rises through the petiole it becomes more curved and takes the form of a C (fig. 14), the edges of which close in toward one another so that a rather narrow opening remains. Meanwhile each of the two protoxylems divides, and from each edge of the C a rather small bundle separates (fig. 15), carrying a single protoxylem. These two bundles rotate so that their xylem groups come to face the C; they constitute the vascular supply of the fertile branch or spike (Chrysler 1910, p. 6). These bundles generally approach one another and for a short distance in their course are fused (fig. 16) edge to edge, but at a higher level separate (fig. 17). (The further branching in fertile and sterile segments will be

Explanation of figures 1–24

In all the figures the stem axis is toward the bottom of the page.

FIGS. 1–8. *Botrychium matricariaefolium*: 1–4, 7, 8, from a series through petiole; figure 4 shows the "parenthesis" stage; figures 5, 6 from another series show the protoxylem groups. Figs. 1–4, 7, ×18. Figs. 5, 6, ×37. Fig. 8, ×14. FIG. 9. *B. Lunaria:* similar to figure 7, but one parenthesis divided before the other. ×22. FIG. 10. *B. matricariaefolium:* same stage as figure 7, bundles leading to fertile branch are larger than the others. ×12. FIG. 11. *B. lanceolatum* var. *angustisegmentum:* slightly earlier stage than figures 7, 10; the bundles form a pseudostele. ×24. FIG. 12. *B. multifidum:* leaf-trace (above) comparable in size with the stele. ×24. FIGS. 13–17. *B. multifidum*, illustrating Plan 1, from series corresponding to figures 1–8. Note absence of stage corresponding to figure 2. Figure 17, through the fertile branch, shows that the fusion in figure 16 is temporary. ×22. FIGS. 18, 19. *B. multifidum*, illustrating Plan 3. Here the division corresponding to figure 2 does occur. ×14. FIG. 20. *B. multifidum:* form of bundle found in fertile branch of certain small individuals. ×86. FIGS. 21–24. *B. dissectum*, illustrating Plan 2. In figure 22 the edges of the petiolar bundle (fig. 21) have fused producing a pseudostele. Figure 24 illustrates the ultimate splitting of the bundle in the fertile branch. ×17.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described later.) The foregoing method of branching, which we may call Plan 1, has been traced in 25 series of *B. multifidum* and varieties and *B. dissectum* and varieties. In three series is seen another mode which will be called Plan 2: the petiolar trace, at first only slightly curved, becomes more and more C-shaped and the gap in the C closes (figs. 21, 22) so that what might be called a solenostele results; this breaks into two unequal pieces lying in the radial plane (fig. 23). The smaller portion runs up into the fertile branch, and may (1) divide into two bundles lying side by side (fig. 24), or (2) become more curved so that it eventually becomes concentric (fig. 20); the latter condition has been observed only in a small plant of *B. multifidum* var. *typicum* collected on an exposed hillside pasture in the Gaspé. In three series still another mode (Plan 3) occurs; the petiolar trace begins as usual as a slightly curved bundle; at about the level of the closing of the basal sheath the trace divides (fig. 18) into a right and left half (in one case the xylem divides but the phloem remains undivided). The bundles rotate so as to face one another; meanwhile they grow and appear like a pair of parentheses from the adaxial ends of which break off the small bundles supplying the fertile segment (fig. 19). This plan is manifestly very similar to the typical behavior of members of *Eubotrychium* and is an interesting link between the two groups.

A partial series through a dried specimen of *B. underwoodianum*, collected in the mountain region of Costa Rica, has been prepared. Toward the base of the petiole the bundle is C-shaped, becoming more triangular as it ascends; the margins curl inward and fuse, producing a deltoid pseudostele; this assumes a more elliptical form and splits into two nearly equal parts, ab- and adaxial, the latter supplying the fertile branch. Whether or not this specimen is typical of the species, its vascular system illustrates Plan 2.

In subgenus *Osmundopteris* (Milde) Clausen, the only representative which has been carefully studied is the common *B. virginianum*. The course of the vascular bundles of the leaf of this species was described in 1910 by the writer, and has been reexamined in the course of the present study. As in the other species, the petiolar trace is at first a curved bundle which becomes definitely C-shaped. At about the level of the top of the basal sheath it splits into a right and a left half (cf. *Eubotrychium*). In many plants a small strand is cut off from the abaxial edge of each of the two petiolar bundles, and strong plants may show further divisions before the region of branching is reached. A short distance below the level at which branching is externally visible, a pair of almost circular bundles break off in the extra-marginal manner to supply the fertile branch (Chrysler 1910, p. 2, 3). A short distance further up in the sterile branch two strands, which may be paired, break off in the same manner to supply the two lowest divisions of the more or less ternate sterile branch. The process is repeated further up in both sterile and fertile branches.

The branching regions from two plants of *B. lanuginosum* (herbarium material) have been made into series. From these it can be made out that the vascular supply of the fertile branch arises extra-marginally as a pair of bundles which face each other and become more or less divided. Branches of the sterile segment also arise extra-marginally.

DISCUSSION

An attempt will now be made to interpret the foregoing observations in terms of Zimmermann's theory of telomes. This is the proposition: the shoot of *Botrychium* consists of a congeries of branches—telomes or mesomes—arising by the process of repeated dichotomy. The first dichotomy separates the leaf from the rhizome (dichotomy I). This is less apparent than the subsequent dichotomies on account of difference in external form of the two resulting mesomes (especially dorsiventrality of at least part of the leaf), also in size and shape of the two branches of the vascular system, viz., solenostele and leaf trace. Probably many of us have entertained the idea of morphological equivalence of the vascular axes in leaf and stem in a fern (e.g., Tansley 1908, p. 130), but Zimmermann definitely enunciates the idea in his paper on the stem (1930a, p. 46 and fig. 5). The difference between stele and leaf trace is largely a relative matter, as may be illustrated by the photograph of a transverse section through the rhizome of *Adiantum pedatum* bearing a large leaf (fig. 26); the uppermost branch of the vascular system is a leaf trace because the series shows that it assumes a C-shape while the lower branch closes the gap and resumes the form of a solenostele. Attention has already been called to an example (fig. 12) in which the size of a leaf trace of *Botrychium* approaches that of the stele. The axial system of *Botrychium* may thus be interpreted as a sympodium, the planes of division being radial, but not in a single plane as are the distal divisions of the sterile branch (fig. 25).

The splitting of the petiolar trace, usually at a slightly higher level than the separation of leaf-base from stem, found in all species of *Eubotrychium*, is here regarded as indicating a second dichotomy (II), although not involving division of the petiole into two mesomes. It should be recalled that distal to this division the vascular system of the leaf in say *B. Lunaria* consists of two parts, right and left, which are independent of each other except at the extreme tip, where fusions occur. Moreover the position assumed by the pair of bundles, namely, facing each other (fig. 4), is what would be expected in case a second dichotomy took place in a plane at right angles to that of dichotomy I. In some species of *Ophioglossum* a single trace may split into an indefinite number of bundles in the common stalk, while in other species the trace may be double from the very outset, i.e., its exit from the stele. The latter condition occurs in *O. Engelmanni* and is illustrated in figure 32; the

double leaf trace is to be seen also in sections of *O. fibrosum* kindly furnished by Professor Maheshwari of Agra, India, and mentioned in his account of this species (1934). It is quite possible that such early splitting of the leaf trace represents a (downward) phylogenetic slide of dichotomy II; the striking differences in level of dichotomy III, culminating in the pronounced upward slide exhibited by *B. lanuginosum* (Chrysler inedit.) may be adduced as evidence supporting this view. The frequency of a pair of bundles in the stipe of Polypodiaceae is not always realized; Waters (1928) found this condition in twelve genera of ferns of the Northeastern States, the chief exceptions occurring in such highly organized genera as *Polypodium, Polystichum* and *Dryopteris*. That the double trace goes far back in the history of fern-like plants is indicated by its occurrence in a number of Paleozoic plants, the classic example being *Lyginopteris* in which Potonié showed that the rachis itself forked (quoted by Scott, 1923, part II, p. 42). It has earlier been argued that the double vascular supply of the fertile branch in *Botrychium* indicates the dual nature of the branch, and forking examples (Chrysler 1910, fig. 28) have been adduced as supporting evidence.

Returning to *B. matricariaefolium*, the third division of the bundles takes place in the radial plane, perpendicular to that of dichotomy II, and is accompanied by the forking of the common axis, resulting in the separation of the fertile and sterile branches; this constitutes dichotomy III. Division of the bundle ("parenthesis") on one side may lag behind that of the other (fig. 9), as might be expected when two axes are concerned. The subsequent dichotomies of sterile and fertile branches are in a plane approximately at right angles to that of dichotomy III (fig. 28). It appears then that in *Eubotrychium* the entire shoot may be interpreted in terms of telomes, the dichotomies alternating in two planes for four divisions after which dorsiventrality is established. Lack of separation of telomes is covered by Zimmermann's term mesome, and is apparently represented by dichotomy II and in many divisions of the distal regions.

In *Sceptridium* the appearance of a single U-shaped bundle in the common stalk, instead of the pair of bundles characteristic of *Eubotrychium*, may be regarded as the result of disappearance of dichotomy II from the ontogenetic series. According to the alternate view, the U-shaped trace would be regarded as primitive and the dual trace as derived. That the first of these alternatives is the more probable is indicated by the following considerations: (1) splitting of the petiolar bundle (dichotomy II) has been found in several individuals (Plan 3) which otherwise belong in *Sceptridium;* (2) there is frequently a marked narrowing of the xylem at the median region of the bundle; (3) two protoxylem groups are present in the bundle of the common stalk; (4) alternation in direction of the divisions to to be expected until dorsiventral structure becomes established; (5) in this subgenus

fusions of the bundles are common at various levels, the most marked and constant case being the temporary fusion immediately after dichotomy III (fig. 16); (6) the condition ultimately reached (e.g., in distal regions of the fertile branch; fig. 17), is essentially the same as in *Eubotrychium*, that is, the leaf has a right and a left half; (7) division often takes place on one side of the U before it occurs on the other side, indicating independence in behavior of the two sides of the U, corresponding to what frequently occurs in the division of the parentheses of *Eubotrychium*.

If on the other hand the condition found in *Sceptridium* is regarded as primitive rather than derived, Plan 2 would probably represent the earliest condition, with the separation of the leaf trace from the stele representing a dichotomy in a radial plane, following by the "repairing" of a solenostele in petiole as well as rhizome, and a subsequent dichotomy of the petiolar solenostele into two C-shaped parts, each of which later undergoes another dichotomy, this time in the plane at right angles to the earlier ones. If this alternative be adopted, Plan 3 would involve the interpolation of a dichotomy of the petiolar trace at about the level at which the petiole breaks off; hence *Eubotrychium* would represent an offshoot from *Sceptridium*. Derivation of Plan 1 from Plan 2 is not so obvious, but it may be remarked that in some of the plants classified as Plan 1 the C-shaped petiolar strand *almost* closes just before the two bundles break off to supply the fertile branch; such cases form a link between Plans 1 and 2—the question is, in which direction are we to read the sequence? If it insisted that the undivided C-shaped trace of *Sceptridium* (vs. the double trace of *Eubotrychium*) represents the primitive condition of the genus, the interpretation of the later branchings of the vascular system in terms of a series of dichotomies becomes strained, and surely we would be safer in regarding the fertile spike as the equivalent of two basal branches (pinnae) of the leaf.

From the standpoints of (1) geographic distribution, (2) the much divided leaves, and (3) type of development of the sporophyte generation, Clausen (1938, p. 22) has argued that *Sceptridium* is the most primitive division of the genus, although he admits that the reflexed type of vernation may be a derived condition. The difficulty in making decisions on such points is illustrated by the fact that the gametophyte of *Ophioglossum* appears to be more primitive than that of *Botrychium*, although the sporophyte of *Ophioglossum* is relatively advanced. Again, it is possible that *Eubotrychium* represents a tendency to reduction in size (consider *B. simplex* var. *tenebrosum*). When writing in 1910 I was much impressed by evidence in favor of this view (*v. infra*, on the extra-marginal origin of leaf traces). But this was several years prior to the appearance of the epoch-making papers on *Rhynia* by Kidston and Lang (1917–21).

In *Osmundopteris* dichotomy I is followed by dichotomy II, as in *Eubo-*

trychium. It is less certain that the cutting off of the small distal strands constitutes another dichotomy, and the extra-marginal method of origin of the strands leading to the fertile branch complicates—although it does not contradict—the interpretation of the origin of the fertile spike as the result of an antero-posterior dichotomy (III).

Marginal and Extra-Marginal Origin of Branch Bundles ("Pinna Traces"). In *Eubotrychium* branching of vascular bundles uniformly takes place as an obvious dichotomy (figs. 8, 28); the bundle is divided, equally or unequally, into two parts by a splitting which passes through xylem and phloem. This mode of division, when occurring in a pinna trace, is called *marginal* by Bower (1923, vol. 1, p. 172). In both sterile and fertile parts of *Sceptridium* and *Osmundopteris*, however, a branch bundle frequently arises not from the edge but from the side of the C (fig. 27), leaving a temporary gap in the C. This mode of origin of a branch trace is called *extra-marginal* by Bower, who speaks of it as characteristic of large leaves. Bower moreover regards the latter method as derivative; this naturally follows if the fern leaf is held to be a sympodium, the evidence for which seems to be overwhelming. The present study has furnished support for the view that the extra-marginal method is characteristic of large leaves, e.g., its occurrence only in *Sceptridium* and *Osmundopteris*. Further, in the latter subgenus this method is found in connection with the origin of the larger (basal) branches in both fertile and sterile segments, while only the marginal method is apt to occur in smaller (distal) branches (cf. Bower's observations on *Trismeria* (1923, p. 173). It is notable that in *Sceptridium* the pair of bundles which supply the fertile spike typically arise strictly from the margin of the much curved C; in only one series, prepared from a plant of *B. dissectum* chosen on account of its having the common stalk 6 mm. in diameter, has even a slight approach to the extra-marginal method been observed at the forking region (figs. 29–31). *Osmundopteris* contains the largest plants of the genus, and it has already been recorded that in *B. virginianum* and *B. lanuginosum* the branch traces in fertile spike as well as pinnae arise extra-marginally.

Although Bower calls attention to the advantage of the extra-marginal method in a large and elaborate leaf, no attempt is made to show how the method may have originated. In view of the many primitive features found in *Ophioglossales* it is not surprising that certain appearances occur which may represent initial stages in the replacement of the marginal method by the extra-marginal. These have been referred to in the paper of 1910, and in the present study numerous additional series have been prepared in order to check the earlier observations. It should be borne in mind that the origin of the pinna trace in *Botrychium* is not so obvious as in some other ferns such as *Todea barbara*, where a pinna trace arises near the "hook" at one

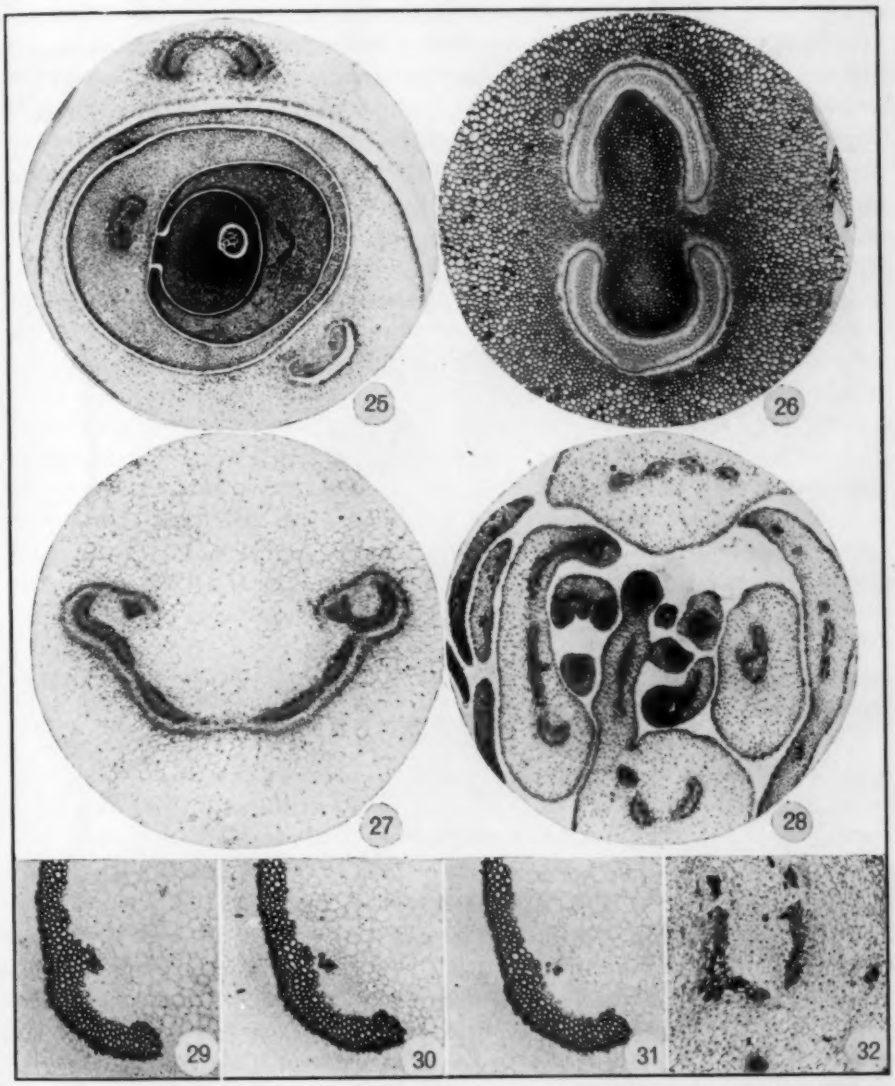

FIG. 25. *B. dissectum:* bud showing five successive leaf bases. ×11. FIG. 26. *Adiantum pedatum:* rhizome showing dichotomy of vascular system at origin of a leaf trace (above). ×15. FIG. 27. *B. multifidum:* fertile branch at origin of lateral branches which arise in the extra-marginal method. ×25. FIG. 28. *B. matricariaefolium:* bud above separation of the sterile branch (above) and fertile branch (below), also vascular supply to several sporangia. ×16. FIGS. 29–31. *B. dissectum*, large plant: edge of C-shaped petiolar bundle just below level of separation of one of the branch bundles supplying the fertile part of leaf (cf. fig. 15); figure 29 is uppermost of the series. See text. ×26. FIG. 32. *Ophioglossum Engelmanni*, rhizome: from upper side of the stele arises a double leaf trace. At lower right appear the two parts of a lower leaf trace. ×28.

side of the C-shaped petiolar trace, leaving a wide gap (Chrysler 1910, fig. 17). In *Botrychium virginianum* the trace arises from the abaxial side of a rather long gap, so that, following a series upward, the appearance presented is that of a small strand branching off from an adaxial edge or hook of the C (Bower 1926, vol. 2, p. 64, also figure 27 of the present paper), swinging around as it rises near the inner face of the C, eventually approaching this and fusing with it at a region somewhat removed from the margin; from this region the bundle constituting the pinna trace now breaks loose and the small marginal strand again becomes the marginal hook of the C. In 1910 I observed that in some of the smaller pinnae of *B. multifidum* (so-called *B. ternatum*) only the upper part of the marginal bundle is present—at the point on the C at which a pinna trace breaks loose a small strand is seen attached on the inner (adaxial) face of the bundle (fig. 29), and a little further down separates, running downward for a short but variable distance, dwindling (figs. 30, 31) and eventually disappearing. Such a strand was in 1910 interpreted as a vestigial structure, for the reason that because of its lack of attachment at its lower end it could not function as a conducting organ. Many additional instances have lately been observed in the fertile and sterile segments in *Sceptridium,* including one instance (mentioned in the preceding paragraph) where each of the two main bundles supplying the fertile spike arises in the manner just described. It is of interest to report also one similar case in the fertile segment of *B. lanceolatum* var. *angustisegmentum.*

But may it not be that these apparent "vestiges" on the contrary represent initial stages in the evolution of the extra-marginal method? At the point where a marginal strand is about to break off it is apt to be distinctly curved, so that a thickening is manifest where the separation occurs; this thickening may be the first step leading to the extra-marginal method. Then might follow the separation of a few tracheids from this thickened region, and the initials of such a group of tracheids might extend downward and at a later stage join the margin of the parent bundle. If this sequence appears fanciful, there are just two other possible modes of origin of the extra-marginal method that occur to the writer; either the pinna trace moved gradually from the margin toward the median region of the parent bundle, or else the new place of origin was assumed as a straight mutation. Perhaps, after all, the observations recorded in the preceding paragraph are best regarded as vestiges. But such a point of view would imply that the large-leaved species are the primitive members of the genus; this would indicate that *B. virginianum,* in which the extra-marginal plan extends to the base of the fertile spike, is the most primitive, that is, we would continue to look for ancestral conditions among the most fern-like species, which I believe is the fundamental objection to the concept of Roeper (1859), who, it will be

recalled, homologized the fertile spike with the two basal pinnae of a fern. It is probable that with Bower (1935, p. 363) we should look for the ancestors of *Ophioglossales* "among those early vascular plants in which the morphological differentiation is less determinate."

In considering these possibilities much appears to depend on whether segregation of fertile from sterile telomes occurred before or after dorsiventrality became established. If this segregation took place at an early stage in the evolution of the genus *Botrychium* we may regard the smaller degree of dorsiventrality (internal as well as external) in the fertile branch as the persistence of an ancestral feature; later the divisions of the sterile mesomes

FIG. 33. *B. simplex* var. *tenebrosum*, abnormal plant. At the right is slightly flattened "sterile" branch bearing five sporangia. Natural size.

became restricted to a single plane, and an efficient photosynthetic organ arose. But if on the other hand dorsiventrality of a shoot consisting of both fertile and sterile telomes appeared at an early period, segregation of two basal branches as spore-bearing organs might follow, as appears to have taken place in *Anemia*. In such an event these two branches would have fused to make the fertile spike, while according to the other alternative the two halves of the fertile region failed to separate.

As to the cases of sporangia on branches of the sterile segment, these are of frequent occurrence in many of the species. The easiest way to interpret these cases is to consider them as reminders of the condition when there was not the sharp segregation into sterile and fertile telomes which now characterizes the order. A particularly interesting example which has come to my attention was collected in Passaic County, N. J., and is probably to be regarded as *B. simplex* var. *tenebrosum* (fig. 33). The "sterile" branch is

small, somewhat fan-shaped, and bears five relatively large sporangia in marginal position; a notch at the tip carries out the plan of a series of dichotomies as does the venation. The fertile branch shows the usual axis (fused telomes), and bears 15 sporangia, each terminating a short telome. This branch, like the sterile segment, has a terminal notch; thus the right and left parts of each branch are indicated. The plant is strangely suggestive of how an ancestral *Botrychium* may have appeared.

SUMMARY

1. Zimmermann has advanced the hypothesis that the fertile spike in Ophioglossales, namely, a branch arising in a plane perpendicular to that of the other divisions, represents a survival of the type of branching found in *Rhynia* and Coenopteridales. This proposal is here tested from the standpoint of vascular anatomy.

2. In subgenus *Eubotrychium* the vascular system of the shoot undergoes a series of four dichotomies in planes radial and tangential alternating with each other. At the third division the fertile and sterile branches separate. With the fourth division dorsiventrality of each branch is established, and subsequent dichotomies are in the same plane.

3. Subgenus *Sceptridium* shows less uniformity and follows one or another of three plans. Generally the second dichotomy (splitting of the leaf-trace) is absent, but transitions occur to the condition typical of *Eubotrychium*. Two possible interpretations are submitted, both in terms of dichotomy; according to the preferred interpretation, the condition in *Sceptridium* is derived from that found in *Eubotrychium*.

4. In both *Sceptridium* and *Osmundopteris* the extra-marginal origin of branch bundles obscures the dichotomous plan, and is regarded as a derived condition.

5. A possible transition from the marginal to extra-marginal mode of origin of branch bundles is described.

6. The bearing of abnormal individuals on the general problem is briefly considered.

7. The possibility of deriving Ophioglossales more or less directly from Psilophytales receives some support from the present investigation. If the evidence should be held sufficient, the hypothesis of Roeper would be abandoned.

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THE BRYOPHYTES OF SHENANDOAH NATIONAL PARK, VIRGINIA

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In June 1944 the authors spent three weeks in Shenandoah National Park, Virginia, in the northern section of the Blue Ridge Mountains, collecting bryophytes. The living quarters used were five Appalachian Trail Club shelters (Range View, Meadow Spring, Rock Spring, Pocosin, and Doyle River) and the collections center around those regions. The areas collected are arranged below from north to south and are cited in that order in the annotated list of species concluding this report.

Little Devils Stairs, Rappahannock County. Altitude 2500–1500 feet. June 20, 1944.
Bear Wallow, Page County. Altitude 3000 feet. June 18, 1944.
Appalachian Trail south of Elk Wallow Gap, Page and Rappahannock Counties. Altitude about 2500 feet. June 19, 1944.
Buck Hollow Trail, Rappahannock County. Altitude 1500–3000 feet. June 13, 1944.
Pinnacle Ridge, Rappahannock County. Altitude 3400–3500 feet. June 14, 1944.
Limberlost, Madison County. Altitude 3200 feet. June 17, 1944.
Old Rag Mountain, Madison County. Altitude 3200 feet. June 17, 1944.
Hawksbill Mountain, Page County. Altitude 3500–4049 feet. June 16, 1944.
Appalachian Trail between Franklin Cliffs and Crescent Rocks, Page County. Altitude 3000–3500 feet. June 15–16, 1944.
Fisher's Gap and Rose River, North Fork, Madison County. Altitude 2500 feet. June 15, 1944.
Appalachian Trail—Pocosin Shelter to Lewis Mountain, Greene County. Altitude 3000–3500 feet. June 23, 1944.
Pocosin Fire Road, Greene County. June 24–25, 1944.
Appalachian Trail—Pocosin Shelter to South River, Greene County. Altitude 300–3500 feet. June 22, 1944.
South River, Greene County. Altitude 3000–2000 feet. June 22–24, 1944.
Big Flat Mountain (altitude 3600 feet), Loft Mountain (altitude 3500 feet), and Ivy Creek (altitude 2500–2000 feet), June 26, 1944.
Doyle River (altitude 3000–1600 feet) and Jones Run (altitude 1500–2800 feet), Albemarle County. June 27, 1944.
Big Run Trail, Rockingham County. Altitude 2750–1500 feet. June 29, 1944.
Big Run Bridge, Rockingham County. June 29, 1944.

All the species reported here were collected along the ridge, and none are from the valleys to the east (the Piedmont) or west (the Great Valley). The Blue Ridge is the exposed core of a large anticline composed of Pre-Cambrian igneous rocks: gneiss, schist, granite, metabasalt. The flanks of the ridge are silicious sedimentary rocks of lower Cambrian sandstone, quartzite, and some slate. The most resistant rocks of the ridge, metabasalt or greenstone, have formed the high ledges projecting several hundred feet above the summit peneplain (3500 feet elevation) and bold monadnocks such as Stony Man (4011 feet) and Hawksbill (4049 feet).

The present ridge has been produced by four periods of erosion alternated with periods of uplift. The remains of three peneplains are apparent as a result of this process and the present valley floor to the west of the Ridge is the product of the present or fourth erosion period. The sedimentary rocks including all the sandstones and limestones which once covered the ridge have been eroded away leaving only the highly resistant igneous core as the present ridge.

The result of these four extended periods of erosion is a highly dissected area with few elevated flat lands. There are few swampy areas, and therefore a limited range of habitats and a restricted diversity of flora. The region is remarkably well drained, with only two small areas which might be called swamps—one in Bear Wallow and the other at Big Meadows. This means that habitats for many aquatic or semi-aquatic bryophytes are lacking in the Park.

The fact that all the rocks in the ridge are igneous eliminates the possibility of finding several score of limestone-inhabiting bryophytes that would normally be expected to occur in the range. Comparison with the only recent extensive study of mosses in Virginia (Patterson 1940a,b, 1943, 1944) shows about 20 species occurring exclusively on limestone at Mountain Lake, Virginia; of these species only three (*Encalypta streptocarpa, Barbula unguiculata,* and *Anomodon viticulosus*) were found in Shenandoah National Park. Only one list of Virginia mosses (Britton 1893) had been published previous to Patterson's work.

The flora of the Blue Ridge is more closely allied with the flora of northeastern North America than with that of the southern part of the continent. Less than ten per cent of the species found in the park are characteristically southern with their northern limit of range in Virginia. Over ninety per cent of all the bryophytes collected are species common in and characteristic of the area from New England to the Great Lakes and the Appalachians.

In the complete lists of 38 species of Hepaticae and 171 species of Musci, which form the main body of this paper, rare species and range extensions are marked with an asterisk. The most interesting mosses and liverworts are listed immediately below with the known range in North America and the adjoining states as given for West Virginia by Ammons (1940) and Tennessee by Sharp (1939).

Hepaticae

PTILIDIUM CILIARE. Greenland to Alaska, south to New England and Minnesota. Not reported in West Virginia, Virginia, or Tennessee.

CEPHALOZIELLA HAMPEANA. Widespread but not collected in West Virginia, Virginia, Tennessee, or in Virginia since 1892 (Haynes 1927).

LOPHOCOLEA MINOR. Quebec to British Columbia, south to Pennsylvania, Indiana, Kentucky, West Virginia, Minnesota, Montana, Idaho, and New Mexico. Not reported in Tennessee or by Sharp (1944) in Virginia; collected once in Virginia by Small (Evans 1893).

CHILOSCYPHUS PALLESCENS. Quebec to British Columbia, south to North Carolina, Kentucky, Tennessee, Idaho, New Mexico, Utah, Oregon, Washington. Not before reported in Virginia. This species was found also near the park headquarters just outside the park boundary.

CHILOSCYPHUS POLYANTHUS. Labrador to Alaska, south to North Carolina, Tennessee, Missouri, Colorado, Utah, and California. Not collected in Virginia since 1892 (Haynes 1927).

CHILOSCYPHUS RIVULARIS. Newfoundland to British Columbia, south to North Carolina, Oklahoma, New Mexico, and California. Not reported in Virginia since 1937 (Bloomquist).

BARBILOPHOZIA BARBATA. Greenland to Yukon, south to New York, New Jersey, and Virginia. Reported by Sharp (1944) as rare at Mountain Lake.

PLAGIOCHILA LUDOVICIANA. Sharp (1944) says of this species, "This rather robust hepatic has not been reported before north of Tennessee and North Carolina." The present specimen from Shenandoah National Park extends the range farther north in Virginia.

Musci

The following species and varieties are believed to be new to Virginia:

FISSIDENS VIRIDULUS. South to the middle Atlantic states; rare in Tennessee.

DITRICHUM LINEARE. Prince Edward Island to S. Carolina and Missouri. Rare in Tennessee.

DICRANOWEISIA CRISPULA. Greenland to Labrador, Mt. Marcy, N. Y., and Mt. Katahdin, Maine.

DICRANELLA VARIA. Not common in Tennessee.

RHACOMITICUM HETEROSTICHUM var. GRACILESCENS Bry. Eur. "Apparently very rare but your specimen checks with *Holzinger 186*, cited as the first American collection," Geneva Sayre.

MNIUM ORTHORHYNCHUM. In the east, south to North Carolina.

THUIDIUM PHILIBERTI. Southern Canada, south to Pennsylvania, New Jersey, and New Mexico.

BRACHYTHECIUM RUTABULUM. Northern North America, south to New Jersey and Pennsylvania; rare in Tennessee.

BRACHYTHECIUM VELUTINUM. Northern North America, south to New Jersey.

CHAMBERLAINIA BIVENTROSA. Known only from Louisiana.

SEMATOPHYLLUM CAESPITOSUM. Rare in Florida.

HYPNUM PALLESCENS. Northern North America, south in the mountains to Tennessee; rare in Tennessee.

HYLOCOMIUM UMBRATUM. Northern North America, south in the mountains to North Carolina; rare in Tennessee.

POLYTRICHUM PILIFERUM. Northern North Amercia, south to New Jersey; rare in Tennessee.

ACKNOWLEDGMENTS

The authors wish to express their appreciation to Dr. E. H. Walker who gave valuable advice in planning the trip, to the Potomac Appalachian Trail Club for the use of their facilities in the Park, to Mr. E. H. Freeland, Super-

intendent of the Park and Mr. W. T. Stephens, Head Ranger, for their valuable assistance and cooperation in Shenandoah National Park.

Identifications have been made by the authors and Dr. Margaret Fulford (Hepaticae), Dr. Winona H. Welch (Frontinalaceae), and Dr. Geneva Sayre (Grimmiaceae). Dr. W. C. Steere has kindly checked doubtful species.

Specimens are deposited in the writers' private herbaria, at Shenandoah National Park, the New York Botanical Garden, and the University of Michigan Herbarium.

In the list of species the nomenclature and arrangement follow Brotherus in the second edition of Engler & Prantl's *Die Natürlichen Pflanzenfamilien* for the Musci and Evans' "List of Hepaticae Found in the United States, Canada, and Arctic America" for the Hepaticae.

HEPATICAE

PTILIDIACEAE

*Ptilidium ciliare (L.) Nees. Little Devils Stairs, Lewis Mountain, Ivy Creek, Doyle River. Morphologically these plants fit the description of *P. ciliare*, but their habitat was not typical. These were collected on logs, whereas *P. ciliare* typically grows on rocks. It is interesting that Sharp (1944) reports *P. pulcherrimum* on rocks instead of its usual substratum of rotten logs.

Ptilidium pulcherrimum (Web.) Hampe. Buck Hollow, Jones Run.

LEPIDOZIACEAE

Microlepidozia sylvatica (Evans) Joerg. Big Run Bridge.

CEPHALOZIACEAE

Cephalozia connivens (Dicks.) Lindb. Big Run.

Nowellia curvifolia (Dicks.) Mitt. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Franklin Cliffs to Crescent Rocks, Rose River, Lewis Mountain, South River, Ivy Creek, Jones Run.

Odontoschisma denudatum (Mart.) Dumort. Bear Wallow, Elk Wallow Gap, Ivy Creek, Jones Run.

CEPHALOZIELLIACEAE

*Cephaloziella hampeana (Nees) Schiffn. Little Devils Stairs, Big Run.

HARPANTHACEAE

Lophocolea bidentata (L.) Dumort. Bear Wallow.

Lophocolea heterophylla (Schrad.) Dumort. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, South River, Ivy Creek.

*Lophocolea minor Nees. Ivy Creek.

*Chiloscyphus polyanthus (L.) Corda. Big Run.

*Chiloscyphus pallescens (Ehrh.) Dumort. Buck Hollow.

*Chiloscyphus rivularis (Schrad.) Loeske. Ivy Creek. Bloomquist (1937) records *C. rivularis* for Mountain Lake, but Sharp (1944) did not collect it again.

JUNGERMANNIACEAE

*BARBILOPHOZIA BARBATA (Schmid.) Loeske. Pinnacle Ridge, Big Run.

JAMESONIELLA AUTUMNALIS (DC.) Steph. Little Devils Stairs, Buck Hollow, South River, Lewis Mountain, Pocosin to South River.

PLECTOCOLEA CRENULATA (Smith) Evans. Little Devils Stairs, Ivy Creek, Big Flat Mountain, Big Run.

MARSUPELLACEAE

MARSUPELLA EMARGINATA (Ehrh.) Dumort. Hawksbill, Franklin Cliffs, Rose River, Pocosin Fire Road, South River, Big Run.

PLAGIOCHILACEAE

PLAGIOCHILA ASPLENIOIDES (L.) Dumort. Little Devils Stairs, Buck Hollow, Jones Run, Doyle River.

*PLAGIOCHILA LUDOVICIANA Sulliv. Little Devils Stairs. Sharp (1944) first reported this species in Virginia, unknown previously north of Tennessee and North Carolina. This collection extends its range farther north in Virginia.

SCAPANIACEAE

DIPLOPHYLLUM APICULATUM (Evans) Steph. Hawksbill, Franklin Cliffs.

SCAPANIA NEMOROSA (L.) Dumort. Little Devils Stairs, Bear Wallow, Buck Hollow, Hawksbill, Franklin Cliffs to Cresent Rocks, Rose River, South River, Pocosin to South River, Ivy Creek, Big Run, Big Run Bridge.

SCAPANIA UNDULATA (L.) Dumort. Bear Wallow, Buck Hollow.

PORELLACEAE

PORELLA PINNATA L. Bear Wallow, Buck Hollow.

PORELLA PLATYPHYLLOIDEA (Schwein.) Lindb. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Hawksbill, Franklin Cliffs, Lewis Mountain, South River, Doyle River.

RADULACEAE

RADULA COMPLANATA (L.) Dumort. Little Devils Stairs, Buck Hollow.

RADULA OBCONICA Sulliv. Buck Hollow.

FRULLANIACEAE

FRULLANIA ASAGRAYANA Mont. Little Devils Stairs, Buck Hollow, Hawksbill, Rose River, Limberlost, Lewis Mountain, South River, Pocosin to South River, Big Run.

FRULLANIA BRITTONIAE Evans. Buck Hollow, Pinnacle Ridge, Hawksbill, Lewis Mountain.

FRULLANIA EBORACENSIS Gottsche. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, Limberlost, Old Rag, Big Meadows, Hawksbill, Rose River, Lewis Mountain, South River, Big Run.

FRULLANIA RIPARIA Hampe. Ivy Creek, Doyle River, Jones Run.

JUBULA PENNSYLVANICA (Steph.) Evans. Little Devils Stairs, Elk Wallow, Buck Hollow, Rose River.

LEJEUNEACEAE

LEUCOLEJEUNEA CLYPEATA (Schwein.) Evans. Buck Hollow, Rose River, Doyle River.

LEJEUNEA CAVIFOLIA (Ehrh.) Lindb. Little Devils Stairs, Buck Hollow, Franklin Cliffs.

LEJEUNEA PATENS Lindb. Little Devils Stairs, Buck Hollow, Doyle River.

METZGERIACEAE

METZGERIA CONJUGATA Lindb. Buck Hollow, Doyle River.

METZGERIA CRASSIPILIS (Lindb.) Evans. South River, Doyle River, Jones Run.

MARCHANTIACEAE

CONOCEPHALUM CONICUM (L.) Dumort. Little Devils Stairs, Ivy Creek.

REBOULIACEAE

REBOULIA HEMISPHAERICA (L.) Raddi. South River.

MUSCI

ANDREAECEAE

ANDREAEA ROTHII Web. & Mohr. Hawksbill.

FISSIDENTACEAE

FISSIDENS ADIANTOIDES Hedw. Little Devils Stairs, Bear Wallow, Buck Hollow, Franklin Cliffs, Jones Run.

FISSIDENS CRISTATUS Wils. Little Devils Stairs, Bear Wallow, Buck Hollow, Franklin Cliffs, Pocosin Shelter to South River, South River, Pocosin Fire Road, Ivy Creek,Doyle River, Jones Run, Big Run.

FISSIDENS MINUTULUS Sull. Elk Wallow, Buck Hollow, Rose River, Old Rag, Ivy Creek, Doyle River.

FISSIDENS OSMUNDIOIDES Hedw. Bear Wallow, Buck Hollow, Franklin Cliffs, Pocosin Fire Road, South River, Loft Mountain, Doyle River, Big Run.

FISSIDENS SUBBASILARIS Hedw. Buck Hollow, Limberlost, Lewis Mountain.

FISSIDENS TAXIFOLIUS Hedw. Bear Wallow, Rose River, South River, Lewis Mountain, Big Run.

*FISSIDENS VIRIDULUS (Web. & Mohr) Wahlenb. Pocosin to South River, South River, Ivy Creek.

DITRICHACEAE

CERATODON PURPUREUS (Hedw.) Brid. Little Devils Stairs, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Hawksbill, Pocosin Fire Road, South River, Lewis Mountain, Big Flat Mountain.

*DITRICHUM LINEARE (Sw.) Lindb. Hawksbill, Jones Run.

DITRICHUM PALLIDUM (Hedw.) Hampe. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Rose River, Hawksbill, Old Rag, Loft Mountain, Ivy Creek, Doyle River, Big Run.

DITRICHUM PUSILLUM (Hedw.) E. G. Britton. Little Devils Stairs, Elk Wallow Gap, Pinnacle Ridge, Franklin Cliffs, Hawksbill, Rose River, South River, Lewis Mountain, Big Flat Mountain, Ivy Creek, Big Run.

DICRANACEAE

DICRANELLA HETEROMALLA (Hedw.) Schimp. Elk Wallow Gap, Pinnacle Ridge, Hawksbill, Limberlost, Old Rag, Fishers Gap, Lewis Mountain, Pocosin to South River, Loft Mountain, Jones Run, Big Run.

*DICRANELLA VARIA (Hedw.) Schimp. Elk Wallow Gap, Pocosin Fire Road.

*DICRAONOWEISIA CRISPULA (Hedw.) Lindb. Pinnacle Ridge, Hawksbill, Ivy Creek.

PARALEUCOBRYUM LONGIFOLIUM (Hedw.) Loeske. Elk Wallow Gap.

RHADBOWEISIA DENTICULATA (Brid.) Bry. Eur. Old Rag, Franklin Cliffs, Crescent Rocks.

DICRANUM BONJEANI DeNot. Franklin Cliffs.

DICRANUM FLAGELLARE Hedw. Bear Wallow, Elk Wallow Gap, Buck Hollow, Rose River, South River, Ivy Creek, Loft Mountain.

DICRANUM FULVUM Hook. Little Devils Stairs, Bear Wallow, Buck Hollow, Hawksbill, Rose River, Franklin Cliffs, Big Meadows, Pocosin Fire Road, South River, Lewis Mountain, Ivy Creek, Big Run.

DICRANUM FUSCESCENS Turn. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Hawksbill, Franklin Cliffs, Rose River, Old Rag, Pocosin Fire Road, South River, Ivy Creek, Big Run.

DICRANUM MONTANUM Hedw. Little Devils Stairs, Buck Hollow, Limberlost, Pocosin Fire Road, South River, Lewis Mountain, Doyle River.

DICRANUM RUGOSUM (Hoffm.) Brid. Franklin Cliffs.

DICRANUM SCOPARIUM Hedw. Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Hawksbill, Franklin Cliffs, Rose River, Pocosin Fire Road, South River, Lewis Mountain, Doyle River, Big Run.

LEUCOBRYACEAE

LEUCOBRYUM ALBIDUM (Brid.) Lindb. Bear Wallow, Lewis Mountain, Big Run.

LEUCOBRYUM GLAUCUM (Hedw.) Schimp. Bear Wallow, Elk Wallow Gap, Buck Hollow, Franklin Cliffs, Rose River, Limberlost, Pocosin Fire Road, South River, Ivy Creek, Doyle River, Big Run, Big Run Bridge.

ENCALYPTACEAE

ENCALYPTA STREPTOCARPA Hedw. Pocosin Shelter to South River, Drive at Big Run Trail.

POTTIACEAE

WEISIA VIRIDULA Hedw. Pocosin Shelter to South River, Doyle River, Big Run.

TORTELLA CAESPITOSA (Schwaegr.) Limpr. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Franklin Cliffs, Rose River, Pocosin Shelter to South River, Jones Run, Doyle River, Big Run.

BARBULA UNGUICULATA Hedw. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Pocosin Fire Road, South River, Ivy Creek, Doyle River, Big Run.

GRIMMIACEAE

GRIMMIA ALPICOLA var. RIVULARIS (Brid.) Broth. Buck Hollow, Old Rag, Rose River.

GRIMMIA APOCARPA Hedw. Pocosin to South River, Doyle River.

GRIMMIA APOCARPA var. CONVERTA (Funck.) Spreng. Crescent Rocks.

GRIMMIA APOCARPA var. GRACILIS (Schleich.) W. & M. Big Run.

GRIMMIA PILIFERA Beauv. Elk Wallow Gap, Little Devils Stairs, Pinnacle Ridge, Limberlost, Lewis Mountain, Doyle River, Big Run.

*RHACOMITRIUM HETEROSTICHUM var. GRACILESCENS Bry. Eur. Crescent Rocks.

FUNARIACEAE

PHYSCOMITRIUM TURBINATUM (Michx.) Brid. Buck Hollow, Pocosin Shelter to South River, Doyle River.

TETRAPHIDACEAE

TETRAPHIS PELLUCIDA Hedw. Little Devils Stairs, Bear Wallow, Rose River, Big Run Bridge.

BRYACEAE

MNIOBRYUM ALBICANS (Wahlenb.) Limpr. [*Pohlia Wahlenbergii* (Web. & Mohr) Andrews]. Buck Hollow, Big Run.

BRYUM ARGENTEUM Hedw. Bear Wallow, Buck Hollow, Pinnacle Ridge, Lewis Mountain.

BRYUM BIMUM Schreb. Little Devils Stairs, Bear Wallow, Buck Hollow, Hawksbill, Franklin Cliffs, Rose River, Lewis Mountain, Pocosin Shelter to South River, Doyle River, Jones Run.

BRYUM CAESPITICIUM Hedw. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, Lewis Mountain, Ivy Creek, Jones Run.

BRYUM CAPILLARE Hedw. Little Devils Stairs, Pinnacle Ridge, Old Rag, Franklin Cliffs, Pocosin Shelter to South River, Doyle River, Big Run.

RHODOBRYUM ROSEUM (Bry. Eur.) Limpr. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Pinnacle Ridge, Old Rag, Hawksbill, Rose River, Pocosin Shelter to South River, Pocosin Fire Road, South River, Lewis Mountain, Jones Run, Big Run.

POHLIA CRUDA (Hedw.) Lindb. Lewis Mountain.

POHLIA NUTANS (Schreb.) Lindb. Buck Hollow.

MNIUM AFFINE Bland. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Hawksbill, Franklin Cliffs, Pocosin Fire Road, Pocosin Shelter to South River, South River, Lewis Mountain, Ivy Creek, Doyle River, Big Run.

MNIUM CUSPIDATUM Hedw. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Pinnacle Ridge, Hawksbill, Pocosin Shelter to South River, South River, Doyle River, Jones Run, Big Run.

MNIUM HORNUM Hedw. Buck Hollow, Big Run Bridge.

MNIUM MARGINATUM (Dicks.) P. B. Little Devils Stairs.

*MNIUM ORTHORHYNCHUM Brid. Little Devils Stairs.

MNIUM PUNCTATUM Hedw. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, Rose River, Ivy Creek.

MNIUM STELLARE Reich. Jones Run.

AULACOMNIACEAE

AULACOMNIUM HETEROSTICHUM (Hedw.) Bry. Eur. Little Devils Stairs, Elk Wallow Gap, Franklin Cliffs, Pocosin Shelter to South River, Doyle River, Jones Run, Big Run.

AULACOMNIUM PALUSTRE (Web. & Mohr) Schwaegr. Little Devils Stairs, Buck Hollow, Pinnacle Ridge.

BARTRAMIACEAE

BARTRAMIA POMIFORMIS Hedw. Elk Wallow Gap, Buck Hollow, Franklin Cliffs, Hawksbill, Pocosin Shelter to South River, South River, Jones Run, Big Run.

*PHILONOTIS AMERICANA Dismier. Big Run Bridge.

PHILONOTIS FONTANA (Hedw.) Brid. Little Devils Stairs, Bear Wallow, Buck Hollow, Pinnacle Ridge, Franklin Cliffs, Pocosin Shelter to South River, South River, Doyle River.

ORTHOTRICACEAE

ORTHOTRICHUM OHIOENSE Sull. & Lesq. Loft Mountain.

*ORTHOTRICHUM SPECIOSUM Nees. Pinnacle Ridge, Old Rag, Big Run.

ULOTA AMERICANA (P. B.) Limpr. Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Limberlost, Old Rag, Hawksbill, Franklin Cliffs, Rose River, Pocosin Fire Road, South River, Lewis Mountain, Ivy Creek, Big Run.

ULOTA CRISPA (Hedw.) Brid. Little Devils Stairs, Limberlost, Old Rag, Big Meadows, Hawksbill, Rose River, Lewis Mountain, Pocosin Shelter to South River, Big Flat Mountain, Loft Mountain, Big Run.

DRUMMONDIA PROREPENS (Hedw.) Jenn. Little Devils Stairs, Pinnacle Ridge, Hawksbill, Crescent Rocks, Lewis Mountain, Pocosin Shelter to South River, Big Flat Mountain, Loft Mountain, Ivy Creek, Jones Run, Big Run.

FONTINALACEAE

FONTINALIS NOVAE-ANGLIAE Sull. Bear Wallow.

CLIMACIACEAE

CLIMACIUM AMERICANUM Brid. Bear Wallow, Buck Hollow, Pocosin Shelter to South River, Big Flat Mountain, Ivy Creek, Doyle River, Jones Run, Big Run Bridge.

CLIMACIUM DENDROIDES (Hedw.) Web. & Mohr. Pocosin Shelter to South River, Doyle River.

CLIMACIUM KINDBERGII (R. & C.) Grout. Big Run Bridge.

POROTRICHUM ALLEGHANIENSE (C. Müll.) Grout. Little Devils Stairs, Buck Hollow, Pocosin Shelter to South River, Lewis Mountain, Jones Run.

HEDWIGIACEAE

HEDWIGIA CILIATA Hedw. Little Devils Stairs, Bear Wallow, Buck Hollow, Pinnacle Ridge, Old Rag, Hawksbill, Franklin Cliffs, Rose River, Pocosin Shelter to South River, Lewis Mountain, Ivy Creek, Big Run.

LEUCODONTACEAE

LEUCODON BRACHYPUS Brid. Hawksbill, Franklin Cliffs, Rose River, Pocosin Fire Road, South River, Big Flat Mountain, Big Run.

LEUCODON JULACEUS f. FLAGELLIFERUS Grout. Ivy Creek.

LEUCODON SCIUROIDES (Hedw.) Schwaegr. Pinnacle Ridge, Limberlost, Old Rag.

LEPTODON TRICHOMITRIUM (Hedw.) Mohr. Buck Hollow, Rose River, Lewis Mountain, Pocosin Shelter to South River, South River, Doyle River.

NECKERACEAE

NECKERA PENNATA Hedw. Rose River, Ivy Creek.

THELIACEAE

THELIA ASPRELLA (Hedw.) Sull. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Hawksbill, Franklin Cliffs, Lewis Mountain, Pocosin Shelter to South River, South River, Doyle River, Big Run.

THELIA HIRTELLA (Hedw.) Sull. Elk Wallow Gap.

FABRONIACEAE

SCHWETSCHKEOPSIS DENTICULATA (Sull.) Broth. Little Devils Stairs, Rose River, Pocosin Shelter to South River, Big Run.

LESKEACEAE

LESKEA OBSCURA Hedw. Rose River, Big Flat Mountain.

LESKEA POLYCARPA (Ehrh.) Hedw. Hawksbill, Lewis Mountain, Pocosin Shelter to South River, Doyle River.

THUIDIACEAE

ANOMODON ATTENUATUS (Hedw.) Hueben. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Limberlost, Old Rag, Franklin Cliffs, Rose River, Big Meadows, Lewis Mountain, Pocosin Shelter to South River, Doyle River, Big Run.

ANOMODON MINOR (P. B.) Lindb. Pinnacle Ridge, Limberlost, Lewis Mountain, Pocosin Shelter to South River, South River, Doyle River, Jones Run.

ANOMODON ROSTRATUS (Hedw.) Schimp. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Rose River, Pocosin Fire Road, South River, Doyle River, Jones Run, Big Run.

ANOMODON RUGELII (C. Müll.) Keissl. Pinnacle Ridge, Crescent Rocks, Rose River, Lewis Mountain, Big Flat Mountain.

ANOMODON TRISTIS (Cesati) Sull. Pinnacle Ridge, Big Flat Mountain.

ANOMODON VITICULOSUS (Hedw.) Hook. & Tayl. Buck Hollow, Old Rag, Hawksbill, Franklin Cliffs, Rose River, Pocosin Shelter to South River, Doyle River, Jones Run.

THUIDIUM ABIETINUM (Brid.) Bry. Eur. Cresent Rocks.

THUIDIUM DELICATULUM (Hedw.) Mitt. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Limberlost, Old Rag, Hawksbill, Franklin Cliffs, Lewis Mountain, Pocosin Fire Road, South River, Big Flat Mountain, Ivy Creek, Doyle River, Big Run.

*THUIDIUM PHILIBERTI Limpr. Big Run.

THUIDIUM SCITUM (P. B.) Aust. Bear Wallow, Elk Wallow Gap, Hawksbill, Rose River, Lewis Mountain, Pocosin Fire Road, South River, Jones Run.

THUIDIUM RECOGNITUM (Hedw.) Lindb. Pocosin Shelter to South River, Big Run.

THUIDIUM VIRGINIANUM (Brid.) Lindb. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Limberlost, Franklin Cliffs, Rose River, Lewis Mountain, Pocosin Fire Road, South River, Ivy Creek, Big Flat Mountain, Doyle River, Jones Run, Big Run.

AMBLYSTEGIACEAE

CAMPYLIUM CHRYSOPHYLLUM (Brid.) Bryhn. Little Devils Stairs, Bear Wallow, Buck Hollow, Franklin Cliffs, Crescent Rocks, Pocosin Fire Road, South River, Jones Run, Big Run.

CAMPYLIUM HISPIDULUM (Brid.) Mitt. Bear Wallow, Elk Wallow Gap, Pinnacle Ridge, Rose River, Lewis Mountain, Pocosin Shelter to South River, Big Run.

*CAMPYLIUM POLYGAMUM (Bry. Eur.) Bryhn. Buck Hollow, South River, Doyle River.

CAMPYLIUM RADICALE (P. B.) Grout. Bear Wallow, Rose River.

*HYGROAMBLYSTEGIUM FLUVIATILE (Sw.) Loeske. Doyle River.

*HYGROAMBLYSTEGIUM FLUVIATILE var. OVATUM Grout. Little Devils Stairs, Elk Wallow Gap, Buck Hollow, Crescent Rocks, Fishers Gap, Pocosin Shelter to South River, Doyle River.

HYGROAMBLYSTEGIUM IRRIGUUM (Wils.) Loeske. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Rose River, Pocosin Shelter to South River, South River, Ivy Creek, Doyle River, Jones Run.

HYGROAMBLYSTEGIUM IRRIGUUM var. SPINIFOLIUM (Schimp.) Grout. Little Devils Stairs, Pocosin Shelter to South River, Ivy Creek, Doyle River.

HYGROAMBLYSTEGIUM ORTHOCLADON (P. B.) Grout. South River, Big Run.

SCIAROMIUM LESCURII (Sull.) Broth. Bear Wallow, Buck Hollow, Rose River, Big Run Bridge.

LEPTODICTYUM TRICHOPODIUM var. KOCHII (Br. & Sch.) Broth. Little Devils Stairs, Big Run.

*AMBLYSTEGIUM JURATZKANUM Schimp. Buck Hollow, Limberlost.

AMBLYSTEGIUM SERPENS (Hedw.) Bry. Eur. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, Big Meadows, Lewis Mountain, Pocosin Shelter to South River, Doyle River.

AMBLYSTEGIUM VARIUM (Hedw.) Lindb. Little Devils Stairs, Bear Wallow, Pinnacle Ridge, Old Rag, Pocosin to South River, Doyle River.

AMBLYSTEGIELLA CONFERVOIDES (Brid.) Loeske. Lewis Mountain.

AMBLYSTEGIELLA SUBTILIS (Hedw.) Loeske. Pinnacle Ridge, Rose River.

HYGROHYPNUM DILATATUM (Wils.) Loeske. Buck Hollow.

HYGROHYPNUM EUGYRIUM (Br. & Sch.) Loeske. Buck Hollow, Ivy Creek.

PLEUROZIUM SCHREBERI (Bry. Eur.) Mitt. Hawksbill.

BRACHYTHECIACEAE

BRACHYTHECIUM ACUTUM (Mitt.) Sull. Jones Run, Doyle River.

BRACHYTHECIUM DIGASTRUM C. Müll. & Kindb. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Pinnacle Ridge, Pocosin Shelter to South River, Jones Run, Big Run.

BRACHYTHECIUM OXYCLADON (Brid.) Jaeger & Sauerb. Little Devils Stairs, Bear Wallow, Old Rag, Franklin Cliffs, Rose River, Lewis Mountain, Pocosin Fire Road, South River, Ivy Creek, Doyle River, Jones Run, Big Run.

BRACHYTHECIUM PLUMOSUM (Sw.) Br. & Sch. Little Devils Stairs, Elk Wallow Gap, Buck Hollow, Hawksbill, Franklin Cliffs, Pocosin Shelter to South River, Ivy Creek, Big Run.

BRACHYTHECIUM RIVULARE Br. & Sch. Little Devils Stairs, Elk Wallow Gap, Buck Hollow, Rose River, Pocosin Shelter to South River, South River, Ivy Creek, Jones Run, Doyle River.

*BRACHYTHECIUM RUTABULUM (Hedw.) Bry. Eur. Bear Wallow, Buck Hollow, Rose River.

BRACHYTHECIUM SALEBROSUM (Hoffm.) Br. & Sch. Elk Wallow Gap, Buck Hollow, Old Rag, Franklin Cliffs, Pocosin Shelter to South River.

*BRACHYTHECIUM VELUTINUM (Hedw.) Bry. Eur. Old Rag.

BRYHNIA GRAMINICOLOR (Brid.) Grout. Little Devils Stairs, Pocosin Shelter to South River.

BRYHNIA NOVAE-ANGLIAE (Sull. & Lesq.) Grout. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Old Rag, Crescent Rocks, Pocosin Shelter to South River, Ivy Creek, Big Run.

CIRRIPHYLLUM BOSCII (Schwaegr.) Grout. Bear Wallow.

CHAMBERLAINIA ACUMINATA (Hedw.) Grout. Rose River, Pocosin Shelter to South River, Big Run.

*CHAMBERLAINIA BIVENTROSA (C. Müll.) Grout. Lewis Mountain, Jones Run.

CHAMBERLAINIA CYRTOPHYLLA (Kindb.) Grout. Jones Run, Doyle River.

EURHYNCHIUM HIANS (Hedw.) Jaeger & Sauerb. Jones Run.

EURHYNCHIUM RUSCIFORME (Nedk.) Milde. Little Devils Stairs, Buck Hollow, Rose River, Pocosin Shelter to South River, South River, Ivy Creek, Doyle River.

EURHYNCHIUM SERRULATUM (Hedw.) Kindb. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Old Rag, Franklin Cliffs, Rose River, Lewis Mountain, Pocosin Fire Road, South River, Doyle River, Big Run.

EURHYNCHIUM STRIGOSUM (Hoffm.) Bry. Eur. Little Devils Stairs, Elk Wallow Gap, Old Rag, Big Run.

EURHYNCHIUM STRIGOSUM var. PRAECOX (Hedw.) Husnot. Little Devils Stairs, Elk Wallow Gap.

ENTODONTACEAE

ENTODON BREVISETUS (Hook & Wils.) Jaeger & Sauerb. Lewis Mountain.

ENTODON CLADORRHIZANS (Hedw.) C. Müll. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Hawksbill, Franklin Cliffs, Rose River, Lewis Mountain, Pocosin Shelter to South River, Pocosin Fire Road, Big Flat Mountain, Jones Run, Big Run.

ENTODON SEDUCTRIX (Hedw.) C. Müll. Elk Wallow Gap, Franklin Cliffs, Crescent Rocks, Lewis Mountain, Pocosin Fire Road, Pocosin to South River, South River, Ivy Creek, Doyle River, Big Run.

PLAGIOTHECIACEAE

PLAGIOTHECIUM DENTICULATUM (Hedw.) Bry. Eur. Little Devils Stairs, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Rose River, Franklin Cliffs, Pocosin Shelter to South River, Ivy Creek, Doyle River, Big Run.

PLAGIOTHECIUM DEPLANATUM (Sull.) Grout. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Rose River, South River.

PLAGIOTHECIUM ELEGANS (Hook.) Sull. Bear Wallow, Old Rag, Franklin Cliffs, Ivy Creek.

PLAGIOTHECIUM LAETUM Bry. Eur. Buck Hollow, Franklin Cliffs, Pocosin Shelter to South River.

PLAGIOTHECIUM MUELLERIANUM Schimp. Limberlost, Pocosin Shelter to South River.

PLAGIOTHECIUM ROSEANUM (Hampe) Bry. Eur. Franklin Cliffs, Pocosin Shelter to South River, Jones Run.

PLAGIOTHECIUM SYLVATICUM (Brid.) Bry. Eur. Little Devils Stairs, Elk Wallow Gap, Buck Hollow, Rose River, Franklin Cliffs, Pocosin Shelter to South River, Doyle River, Jones Run.

PLAGIOTHECIUM TURFACEUM (Lindb.) Lindb. Rose River, Ivy Creek, Doyle River, Big Run.

SEMATOPHYLLACEAE

HETEROPHYLLUM HALDANIANUM (Brev.) Kindb. Buck Hollow, Pinnacle Ridge, Franklin Cliffs, Pocosin Shelter to South River, Lewis Mountain.

BROTHERELLA DELICATULA (James) Fleisch. Pinnacle Ridge, Franklin Cliffs.

BROTHERELLA RECURVANS (Michx.) Fleisch. Big Run.

*SEMATOPHYLLUM CAESPITOSUM (Hedw.) Mitt. Elk Wallow Gap, Rose River, Doyle River.

SEMATOPHYLLUM CAROLINIANUM (C. Müll.) E. G. Britton. Buck Hollow, Pinnacle Ridge, Ivy Creek.

SEMATOPHYLLUM MARYLANDICUM (C. Müll.) E. G. Britton. Buck Hollow.

HOMOMALLIUM ADNATUM (Hedw.) Broth. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Old Rag, Hawksbill, Crescent Rocks, Rose River, Lewis Mountain, Pocosin Shelter to South River, Big Flat Mountain, Ivy Creek, Doyle River, Big Run.

HYPNUM ARCUATUM Lindb. Bear Wallow.

HYPNUM CUPRESSIFORME Hedw. Bear Wallow, Buck Hollow, Rose River, Pocosin Shelter to South River, Ivy Creek, Doyle River.

HYPNUM CURVIFOLIUM Hedw. Bear Wallow, Buck Hollow, Rose River, Hawksbill, Franklin Cliffs, Pocosin Fire Road, South River, Ivy Creek, Jones Run.

HYPNUM FERTILE Sendt. Bear Wallow, Elk Wallow Gap, Hawksbill, Pocosin Fire Road, Big Run.

HYPNUM IMPONENS Hedw. Bear Wallow, Elk Wallow Gap, Pinnacle Ridge, Rose River, Pocosin Shelter to South River, Loft Mountain, Big Run.

HYPNUM MOLLUSCUM Hedw. Buck Hollow, Pinnacle Ridge.

*HYPNUM PALLESCENS (Hedw.) Bry. Eur. Franklin Cliffs, Pocosin Fire Road, South River, Jones Run, Doyle River, Big Run.

HYPNUM REPTILE Michx. Little Devils Stairs, Hawksbill, Pocosin Fire Road, South River, Big Run.

PYLAISIA INTRICATA (Hedw.) Bry. Eur. Bear Wallow, Old Rag, Hawksbill, Franklin Cliffs, Lewis Mountain, Pocosin Shelter to South River, South River, Big Flat Mountain, Doyle River.

PYLAISIA SELWYNII Kindb. Limberlost, Hawksbill, Pocosin Shelter to South River, Big Flat Mountain, Big Run.

RHYTIDIACEAE

RHYTIDIADELPHUS TRIQUETRUS (Hedw.) Warnst. Franklin Cliffs.

RHYTIDIUM RUGOSUM (Hedw.) Kindb. Franklin Cliffs, Pocosin Shelter to South River.

HYLOCOMIACEAE

HYLOCOMIUM BREVIROSTRE (P. B.) Bry. Eur. Franklin Cliffs, Hawksbill, Pocosin Shelter to South River.

HYLOCOMIUM SPLENDENS (Hedw.) Bry. Eur. Franklin Cliffs.

*HYLOCOMIUM UMBRATUM (Hedw.) Bry. Eur. Pocosin Shelter to South River.

DIPHYSCIACEAE

DIPHYSIUM FOLIOSUM (Hedw.) Mohr. Little Devils Stairs, Buck Hollow, Pinnacle Ridge, Hawksbill, Rose River, Lewis Mountain, Ivy Creek, Doyle River.

POLYTRICHACEAE

ATRICHUM ANGUSTATUM (Brid.) Bry. Eur. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Limberlost, Old Rag, Hawksbill, Lewis Mountain, Pocosin Fire Road, South River, Ivy Creek, Big Run.

ATRICHUM ANGUSTATUM var. PLURILAMELLATUM (Jennings) Frye. Jones Run, Doyle River, Big Run.

ATRICHUM MACMILLANI (Holz.) Frye. Buck Hollow.

ATRICHUM UNDULATUM (Hedw.) Beauv. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Limberlost, Old Rag, Hawksbill, Lewis Mountain, Pocosin Fire Road, Pocosin Shelter to South River, Big Flat Mountain, Ivy Creek, Big Run.

POGONATUM PENSILVANICUM (Hedw.) Paris. Little Devils Stairs, Buck Hollow, Hawksbill, Franklin Cliffs, Pocosin Shelter to South River, Big Flat Mountain, Loft Mountain, Ivy Creek, Doyle River, Big Run.

POLYTRICHUM COMMUNE Hedw. Old Rag.

POLYTRICHUM JUNIPERINUM Hedw. Little Devils Stairs, Big Flat Mountain.

POLYTRICHUM OHIOENSE Ren. & Card. Little Devils Stairs, Bear Wallow, Elk Wallow Gap, Buck Hollow, Pinnacle Ridge, Old Rag, Hawksbill, Rose River, Lewis Mountain, Pocosin Fire Road, South River, Ivy Creek, Doyle River, Big Run.

*POLYTRICHUM PILIFERUM Hedw. Hawksbill.

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THE TAXONOMY OF THE GENUS SAUVAGESIA (OCHNACEAE)

JOHN D. DWYER

From the viewpoint of floral structure perhaps no genus of the tribe Luxemburgieae (Ochnaceae),[1] with the possible exception of *Tyleria* Gleason, is more interesting than the herbaceous or suffrutescent genus of the New World *Sauvagesia* L.[2] Not only is the character of the androecium in particular of morphological significance but it is perhaps the most obvious structural feature linking this genus with many of the other genera of the tribe. It is composed of a whorl of five discrete petaloid segments (interior corona) enclosing a regular whorl of five stamens, the interior corona itself encompassed usually by one or several rows of small polymorphic segments (exterior corona). Three genera of the tribe: *Lavradia* Vell., *Leitgebia* Eichl., and *Tyleria* Gleason have a well-defined interior corona. *Lavradia* has five petaloid segments fused into an urceolate cup; the five much reduced androecial segments of *Leitgebia* are united at the base to form a cup-like structure around the ovary; *Tyleria*, on the other hand, has an interior corona of ten uniseriate segments, five of which are large and petaloid and united basally into a cup and the other five of which are smaller and spatulate or obovoid, alternating individually with the larger segments. In addition to the androecium the close relationship of this quartet is also manifested by their elongate subulate style borne atop a tricarpellate carnose and subrotund ovary, as well as by the scarious sepals which persist on the mature scarious capsules, the latter bearing non-alate seeds (except in *Tyleria*). The genus *Poecilandra* Tulasne seemingly links the above complex to *Blastemanthus* Planch., and thus to some of the more remote genera of the Luxemburgieae: *Cespedezia* Goudot, *Godoya* R. and P., *Krukoviella* A. C. Smith, and *Rhytidanthera* van Tieghem, all of which are arborescent and characterized by crassate sepals, subestylate secund crassate pistils with radially arranged stigmas, and coriaceous capsules with alate seeds. I have discussed the relationship of *Poecilandra* and *Blastemanthus* to this latter complex in a previous paper.[3]

[1] This paper was submitted as part of a thesis on the *American Genera of the Tribe Luxemburgieae* (Ochnaceae), in partial fulfillment of the requirements for the degree of Doctor of Philosophy, Biological Laboratories, Fordham University Graduate School, New York, N. Y.

[2] *Sauvagesia erecta* occurs in Africa, where it has probably been introduced.

[3] Bull. Torrey Club 71: 175–178. 1944.

TAXONOMIC HISTORY OF THE GENUS SAUVAGESIA

Sauvagesia, described originally by Linnaeus (Sp. Pl. **1**: 203. 1753), was made the type genus of the Violarieae by Gingins (9) and maintained in the Violaceae by Meissner (12) and Bentham and Hooker (4). Subsequently, St. Hilaire (14) and Martius and Zuccharini (11) placed it in the Frankeniaceae and Droseraceae respectively. Planchon (13) was the first to relate it to the Ochnaceae. Baillon (2), in turn, although placing *Sauvagesia* in the Violaceae as a tribe, related this family to the Ochnaceae. A distinct family Sauvagesiaceae (or *ordo distinctus* Sauvagesieae) was proposed by Bartling (3) and accepted by Grisebach (10), Endlicher (6), Eichler (5), and van Tieghem (15), the first two workers relating the family to the Guttiferae, Frankeniaceae, and Hypericaceae, while Eichler placed the family in the Parietales near the Violaceae. Engler (7) concluded the 19th century history of *Sauvagesia* by uniting it to the Ochnaceae as a subtribe of the Luxemburgieae, the subtribal division being subsequently discarded by Gilg in his recent (8) survey of the Ochnaceae. I concur with Gilg's opinion.

THE ANDROECIUM OF SAUVAGESIA

As indicated previously the staminodia are especially significant in the Sauvagesias. Heretofore no attention has been directed to a character of the segments of the inner corona which is common to most of the species of the genus and itself of evolutionary importance: the vertical submedian ventral ridge and corresponding dorsal furrow of each segment (also found in all the species of *Leitgebia* and *Tyleria*). With the discovery of *S. deficiens* Smith and *S. smithiana* Dwyer the variability of this character becomes evident. Coupled with the fact that the segments of the inner corona of both of these species, which are endemic to the Pacaraima Mountains on the British Guiana-Venezuela border, are obviously broader than those of the remaining species of the genus is the fact that the median ridge is not present but is replaced by two to several well-spaced and irregular-ascending veins arising from the base of each segment. This in my opinion, represents a primitive condition in the evolutionary trend of the genus.

Studies have shown that the presence or absence of the segments of the exterior corona, numbers of whorls and segments, and fasciculate character of the segments cannot be relied upon as stable and constant specific characters. Not only have I been unable to segregate several species hitherto considered distinct (e.g., *S. fruticosa* Mart. and Zucc. and *S. angustifolia* Ule) from *S. sprengelii* St. Hil. on the basis of vegetative characters, but also on the nature of the outer corona. Both Eichler (5) and Gilg (8) employed the latter as a main character in their keys to species. Numerous dissections, however, have made it clear that the segments of the exterior corona range from being densely fasciculate to being completely suppressed. Since this condi-

tion was often found to occur in different flowers from the same plant, its intraspecific value becomes doubtful. Similar variations of the exterior corona are to be found in the more widely collected species *S. erecta* L. and *S. brownei* Planch.

As for the interior corona, observations, particularly on the staminodia of *S. brownei*, indicate that this whorl probably represents a fusion of segments similar to those of the exterior corona, since this species shows frequently the basal parts of the segments fused into a single petaloid segment with the swollen capitate portions free. Upon dissecting a flower of one specimen (*Archer 1809*, NY), it was found that one segment of the interior corona bore a small lateral anther-like appendage.[4] Another flower from this specimen showed one of the segments of the interior corona bearing a basal and lateral falcate appendage similar to those found at the base of the free inner portions of the corona of *Tyleria floribunda* Gleason.

Despite the instability in the presence, number, and fasciculate character of the staminodia of the outer corona these manifest remarkable constancy in their *morphology* except in *S. brownei*. This species, confined to the West Indies, is obviously related to *S. erecta*, particularly in having the bostryches of flowers extending in most cases, to the middle of the stem. The frequent fusion among staminodial segments of the same whorl of *S. brownei* make it probable that this species is experiencing a transitional period in its evolution. This apparent attempt to effect a complete fusion of the parts of these whorls approaches the condition found in the species of *Lavradia*, *Tyleria*, and *Leitgebia*.

GEOGRAPHICAL DISTRIBUTION AND ECONOMIC IMPORTANCE OF SAUVAGESIA

Of the sixteen species of *Sauvagesia* one is pantropical—*S. erecta* L.; one is endemic to the West Indies—*S. brownei* Planch.; three are comparatively well distributed through northern South America and scattered throughout the West Indies—*S. erecta* L., *S. tenella* Lam., and *S. sprengelii* St. Hil. The remaining species are endemic to the Pacaraima Mountains and are localized in distribution.

Apparently the Sauvagesias are of little economic importance. Saint Hilaire (14) and Eichler (5), doubtlessly basing their statements on the notes of previous writers, e.g., Aublet (1), note that the mucilaginous exudate of the weed *S. erecta*, termed by various workers "Ironweed," "Herb of St. Martin," and "Adima" is used as a balm on inflamed portions of the body as well as internally as a purgative.

[4] In my opinion, which is based on observations of abnormal segments of the inner corona, the median ridge of the inner corona is homologous with the filaments of the stamens and the lamina of the segments homologous with the thecae. Similar and more striking instances of the intimate relationship between the stamens and the segments of the interior corona may be found in the closely related family Violaceae.

SAUVAGESIA L. Sp. Pl. **1**: 203. 1753.

Sauvagea Neck. Elem. **2**: 378. 1790.
Roraimanthus Gleason, Phytologia **1**: 39. 1933.

Herbs; branches smooth, glabrous, the stem rarely simple; roots fibrous; leaf-blades subsessile, entire or glandular-serrate, the teeth minute, often revolute or curled, the costa prominent above and below, the secondary veins sharply ascending and prominent; stipules persistent, the cilia few to many,

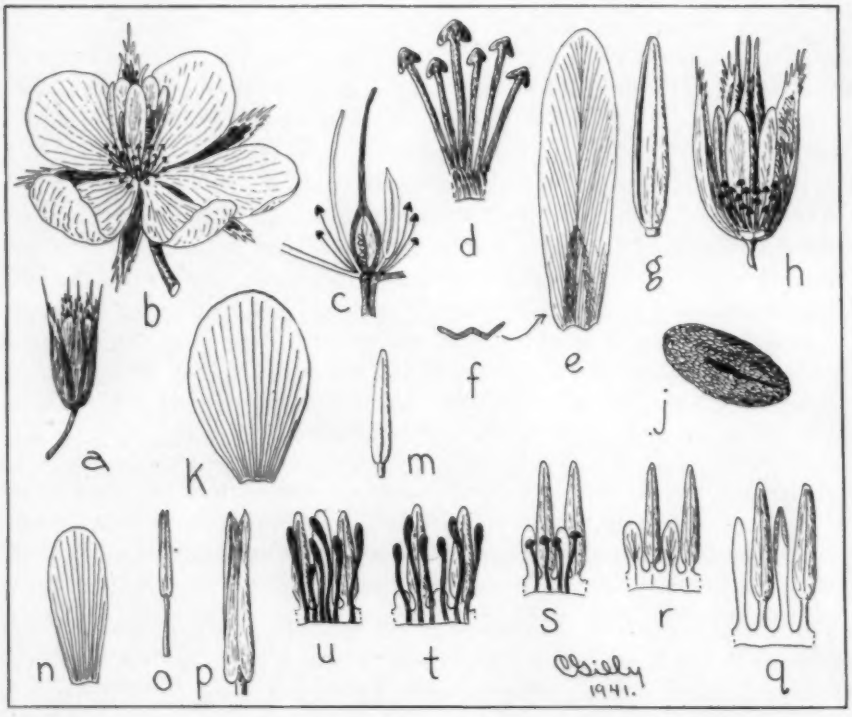

FIG. 1. *Sauvagesia longifolia* Eichl.: *a*—bud (×3); *b*—flower (×3); *c*—longitudinal section through flower (×6); *d*—portion of outer coronal ring (×10); *f*—cross section through the basal portion of inner corona segment, the dorsal face downward; *g*—stamen, showing longitudinal dehiscence of thecae (×10); *h*—capsule, with two of the persistent sepals removed, showing the persistent coronas (×4); *j*—seed (×20). (Drawn from *Tate 1314*.) *S. smithiana* Dwyer: *k*—coronal segment (×10); *m*—stamen (×10). (Drawn from *Tate 321*, TYPE.) *S. tenella* Lam.: *n*—coronal segment (×10); *o*—stamen (×10); *p*—anther, showing free apical portion of the thecae (×20). (Drawn from *Allen 830*.)

filiform, sharply ascending; flowers 2–6 in bostryches or solitary on a shortened axillary peduncle or solitary on short pedicels, the bostryches fasciculate in the axils of the uppermost leaves or borne on a paniculate rachis or axillary in the stem leaves; sepals 5, quincuncial, expanded at anthesis, appressed and persistent in fruit; petals 5, imbricate in bud, red white or violet, soon

deciduous, usually clawed at base; segments of exterior corona present or absent, numerous or rarely few, in 1–3 continuous whorls or fasciculate and opposite to the stamens, unequal, often heteromorphic and in same whorl as stamens, usually filamentous, clavate, anchor-shaped or reniform at apices, shorter than segments of interior corona, persistent in fruit; segments of interior corona 5, free, petaloid, obovate, elliptic, rotund or rarely subulate, shorter than petals in length, with or without a distinct ventral ridge and dorsal furrow, the veins flabellate and subprominent, persistent in fruit; stamens 5, persistent in fruit, the anthers narrow-oblong (rarely subrotund or ovate), rarely exceeding segments of interior corona in length, obtuse or subcordate at base, 4-celled, dehiscing longitudinally, the filaments short (or rarely exceeding anthers in length); ovaries conic, 3-lobed, the styles subulate, the stigmas indeterminate, the ovules borne on 3 parietal placentae extending up most of wall of ovary; capsules turgid, drying dark-brown, irregular-striate, ovate to ovate-elliptic, equal to or exceeding persistent sepals, acute at apices, the styles eventually deciduous, the seeds plump, oblong, and reticulate (fig. 1).

TYPE SPECIES: *Sauvagesia erecta* L. This plant, a common pantropical weed, is perhaps the best known species of the genus and of the tribe Luxemburgieae.

The author wishes to thank the Directors of the institutions listed below who are kind enough to allow him to examine herbarium material of *Sauvagesia*. For purposes of citation a letter designating the institution is used:

Chicago Museum of Natural History, Chicago, Ill. (F).
New York Botanical Garden, New York, N. Y. (NY).
United States National Herbarium, Washington, D. C. (US).

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KEY TO SECTIONS

Exterior corona (when present) heteromorphic; interior corona heteromorphic, the segments alternating (or seemingly so) with the stamens; flowers few in axillary bostryches. 1. *Browneae.*

Exterior corona (when present) regular; interior corona regular, forming 1–3 distinct whorls outside the stamens; flowers few to numerous, rarely solitary, usually in terminal or axillary bostryches.

Flowers solitary on a short bracteolate peduncle. 2. *Imthurnianae.*

Flowers borne in bostryches (in one species simply solitary and axillary).

Anthers oblong, subsessile.

Segments of interior corona oblong or obovate, the median longitudinal furrow and ridge distinct. 3. *Longifoliae.*

Segments of the interior corona subrotund, without a median ridge and furrow. 4. *Smithianae.*

Anthers ovoid (in *S. tenella* oblong), the filaments almost equal to or exceeding the anthers in length. 5. *Linearifoliae.*

KEY TO THE SPECIES

1. *Browneae*

Staminodial segments heteromorphic. 1. *S. brownei.*

2. *Imthurnianae*

Flowers solitary on a short bracteolate peduncle. 2. *S. imthurniana.*

3. *Longifoliae*

Bostryches in the axils of the leaves at least above the middle of the stem.
Leaves oblong-lanceolate, the middle leaves up to 2 cm. long, gradually tapering at the base. 3. *S. erecta.*
Leaves broadly lanceolate, the middle leaves up to 4 cm. long, tapering acutely at the base. 4. *S. grandifolia.*
Bostryches aggregated in a strictly terminal inflorescence.
Inflorescence racemiform; pedicels at least 0.5 mm. wide; sepals 3–6 cm. long, ascending.
Leaves lanceolate, linear-lanceolate or oblong-lanceolate, 0.8–12 cm. long, ascending.
Leaf-blades without prominent secondary veins, the latter arcuate-ascending, joining the costa at a wide angle.
Median leaves 7–12 cm. long, lanceolate, acute at apices; leaf-margins not conspicuously callose; stipules obtuse and non-fimbriate at base. 5. *S. elata.*
Median leaves 2.5–3.5 cm. long, oblong-lanceolate, round-obtuse at apices, the margins distinctly callose-revolute; stipules fimbriate-ciliate at base. 6. *S. racemosa.*
Leaf-blades striate with prominent secondary veins, the latter joining the costa at an acute angle.
Leaves 1.1 cm. or less in length, crowded; apices of sepals ciliate or eciliate. 7. *S. sprengelii.*
Leaves 3–9 cm. long, well-spaced; apices of sepals ciliate (about 2 mm. long). 8. *S. longifolia.*
Leaves ovate, up to 0.7 cm. long, somewhat deflexed. 9. *S. amoena.*
Inflorescence paniculate; pedicels up to 0.2 mm. wide; sepals 2–2.5 mm. long. 10. *S. ramosissima.*

4. *Smithianae*

Sepals unequal, mostly erose-marginate at the apex; veins of segments of interior corona numerous and parallel-ascending. 11. *S. deficiens.*
Sepals equal, acuminate at apex; veins of the segments of interior corona 3+, branching obliquely above the middle. 12. *S. smithiana.*

5. *Linearifoliae*

Leaves linear, stiff, coriaceous; exterior corona present.
Leaf-blades ascending; flowers fasciculate in racemes (anthers elongate, ovoid); sepals with a long terminal cilium subtended by long marginal cilia. 13. *S. linearifolia.*
Leaf-blades deflexed; flowers few, terminal, solitary in the axils of the uppermost leaves; anthers linear-ovate, abruptly apiculate at the apex. 14. *S. deflexifolia.*
Leaves not linear, membranaceous or grandular-fleshy; exterior corona absent.
Stipules not glandular-jointed; anthers oblong; secondary veins of leaves inconspicuous above. 16. *S. tenella.*
Stipules with cilia bearing glandular-joints; anthers subrotund or ovate; secondary veins of leaves inconspicuous above. 15. *S. pulchella.*

1. SAUVAGESIA BROWNEI Planch. in Urban Symb. Ant. 5: 430. 1908.

Sauvagesia stenophylla Urban, Repert. Sp. Nov. 22: 39. 1925.
Sauvagesia microphylla Urban, Repert. Sp. Nov. 22: 39. 1925.

Woody herbs, 5–45 cm. high; branches basal, smooth, elongate or short and densely foliose; petioles up to 2 mm. long; leaf-blades crowded or up to 1 cm. apart, chartaceous, often stiff, the lamina distinctly revolute or plane, elliptic or linear-elliptic, 0.4–1.9 cm. long, at least twice as long as broad, acute at apex, subcuneate at base, the margin callose, the teeth minute and glandular, the secondary veins subprominent above, oblique-ascending; stipules narrow-triangular, the cilia elongate, ascending, arranged in threes at apices of stipules; flowers usually 2 per bostryx, axillary in uppermost leaves, the fascicles (or flowers seemingly solitary) extending to middle of stem, the pedicels shorter than or up to twice length of buds; sepals subequal, lanceolate or elliptic-oblong, 2.5–4.5 mm. long, acute and terminating in a long cilium up to 1.5 mm. long, the veins 5–7; petals obovate-rotund, narrow-obovate or broadly elliptic, 2.5–5 mm. long, equal to or exceeding sepals in length; segments of exterior corona present or absent, numerous to few, in continuous whorls or fascicles, often seemingly in same whorl as stamens, reniform-capitate to subulate, smaller than, equal to or exceeding segments of interior corona in same whorl as stamens and alternate with them, polymorphic (often in same flower), mostly linear, subulate, lanceolate or oblong, up to 1.2 mm. long, acute, obtuse or rostrate at apex; anthers linear, 1.2–1.8 mm. long, the filaments up to 0.8 mm. long, never more than half the length of anthers; ovaries narrowly or widely ovate, 0.7–1.2 mm. long, the styles subulate, 0.8–1.2 mm. long; capsule ovate-oblong, equal to or exceeding sepals in length (fig. 1, *q–u*).

TYPE LOCALITY: Between Mt. Diable and Mt. St. Ann, Jamaica.

DISTRIBUTION: Cuba and Jamaica.

CUBA: Without locality, *Wright 2130* (NY); Pinar Del Rio, Laguna Santa Maria, *Britton, Britton,* and *Earle 7168* (NY); Sierra de Cabra, *Britton, Britton,* and *Gager 7286a* (NY); Savanna de Herradura, *Britton, Britton, et al. 6467* (NY); San Juan y Martinez, *Ekman 18056* (NY, type collection of *S. microphylla*); Herradura, *van Hermann 566* (NY); Guane, *Leon* and *Roca 7021* (NY); Arroyo Galiano, *O'Donovan 5228* (NY); Luis Lazo, *O'Donovan 5296* (NY); Laguna Jovero, *Shafer 10748* (NY), *10865* (NY); Guane, *Shafer 10507* (NY); Without locality, *Shafer* and *Leon 3412* (NY); Isle of Pines: Nueva Gerona, *Curtiss* s. no. (NY); Nueva Gerona, *Jennings 657* (NY); Santa Clara: La Cunagua, *Britton, Britton* and *Wilson 14551* (NY); Cienfuegos, *Combs 435* (NY); Without locality, *Leon 6403* (NY); Banao Mts., Naranjo China, *Leon* and *Roca 8079* (NY); Manacas, *Leon* and *Cazanas 5895* (NY); Lomas de Banao, *Luna 131* (NY); Oriente: Sierra de Nipe, *Ekman 2691* (NY); Arroyo del Medio, *Shafer 3640* (NY), Baracoa, *Underwood* and *Earle 1355* (NY). JAMAICA: Without locality, *Alexander* s. no. (NY); Moody's Gap, *Britton 3369* (NY); Dolphin Head, *Britton* and *Hollick 2200* (NY); Caselton Garden, *Fawcett 8003* (NY); Bradau Hill Rd., *Fawcett 8470* (NY); Upper Clarendon, *Harris 12256* (NY); Portland, *Maxon* and *Killip 96* (NY); Prospect Hill, *Thompson* (F); Bull Head, *Underwood 3363* (NY).

S. brownei, on the basis of vegetative characters, shows strong affinity with *S. erecta*. Examination and dissection of many flowers of both species have shown, however, that the staminodial segments of the former species are heteromorphic while those of the latter are consistently homomorphic. The isolation of *S. brownei* in the West Indies is also suggestive of the distinctness of the species.

S. microphylla and *S. stenophylla*, both described by Urban, lack characters sufficiently strong to warrant giving these species specific rank. They are

probably mere ecological variants which on superficial examination appear to be different from *S. brownei*.

2. SAUVAGESIA IMTHURNIANA (Oliver) Dwyer, Bull. Torrey Club **67**: 291. 1940.

Leitgebia imthurniana Oliver, Trans. Linn. **2**: 271. 1877.
Roraimanthus imthurnianus (Oliver) Gleason, Phytologia **1**: 39. 1933.

Small shrubs, ericoid in habit, up to 30 cm. high; branches patent and angular-ascending; stem nigrescent and rough with persistent bases of stipules; leaf-blades imbricate at summit of branches, sessile, coriaceous, obovate-oblong or sublanceolate, about 9 mm. long, 2–3.5 mm. wide, obtuse at apex and base, the margins callose, glandulose-serrulate above middle, the costa prominent above and below, the secondary veins striate, ascending at a sharp angle; stipules scale-like, deltoid to deltoid-lanceolate, 1.5–2.7 mm. long, the cilia strongly ascending; flowers large, about 1.8 cm. wide at anthesis, terminal, 1–3, one usually persistent on peduncle, the latter arising from the axils of uppermost leaves, up to 1 cm. long, bearing four whorled alternate bracts, the uppermost fertile, the pedicels 1.5–2.8 mm. long, the lower pair long-ciliate toward apex, ensheathing stem in a three-quarter circle, the upper pair long-ciliate and tripartite; sepals unequal, lanceolate, 5.7–7.5 mm. long, 1.5–1.8 mm. wide, acute and minutely erose-glandular at apex, obtuse at base, the base with distinct dorsal glandular areas, the margins entire or minute-scabrid; petals equal, pink, obovate, about 6.5 mm. long, about 4.7 mm. wide, obtuse at apex and base, rounded at point of articulation, the veins slender, evanescent, scarcely flabellate; segments of interior corona subplane, narrow-rectangular or obovate-rectangular, 3.7–3.9 mm. long, 0.9–1 mm. wide, obtuse-rotund at apex, tapering slightly toward base, the longitudinal ridge distinct, the furrow scarcely distinct; anthers oblong-rectangular, 1.3–1.5 mm. long, apiculate (the apiculum 0.2–0.25 mm. long), the filaments about 0.65 mm. long; ovaries ovate-conical, about 2 mm. long; carpels glandular, smooth, ovate-triangular, shorter than or equal to sepals in length, about 2 mm. wide, the apices of carpels reflexed at anthesis, dehiscing at least to middle, the veins few, subprominent, well spaced, branching laxly.

TYPE LOCALITY: Summit of Mt. Roraima, British Guiana-Venezuela boundary line.

DISTRIBUTION: Known only from the summits of Mt. Roraima and Mt. Auyan-Tepui, British Guiana-Venezuela.

BRITISH GUIANA–VENEZUELA BOUNDARY LINE: Summit of Mt. Roraima, *Pinkus 116* (NY); *Tate 400* (NY); Mt. Auyan-Tepui, *Tate 1130* (NY).

Undoubtedly the strongest specific characters of *S. imthurniana* are to be found in the stipules and inflorescence. I consider the multi-bracted stalks of the flowers to be peduncles, which by the almost complete abortion of the flowers become pedicellary in nature.

3. SAUVAGESIA ERECTA L. Sp. Pl. **1**: 203. 1753.

Sauvagesia adima Aubl. Hist. Pl. Guian. Fr. **1**: 251. 1775.
Sauvagesia peruviana R. and S. Syst. Veg. **5**: 457.
Sauvagesia nutans Pers. Syn. Pl. **1**: 253. 1805.

Sauvagesia gemininiflora Sess. and Moc. ex Ging. in DC Prodr. **1**: 315. 1824.
Sauvagesia rubiginosa St. Hil. Mém. Mus. **11**: 101. 1824.
Sauvagesia laxa Mart. and Zucc. Nov. Gen. **1**: 38. 1824.

Woody herbs or subshrubs, 5–60 cm. tall, simple or branching profusely, often bushy in habit or with elongate lax branches; stem rubescent, rough (when lower leaves deciduous) with remnants of stipules; petioles scarcely measureable or up to 5 mm. long; leaf-blades well-spaced or crowded into loose or dense clusters, papyro-membranaceous, often stiff (especially the very narrow leaves), striate, oblong-lanceolate, 1.2–6 cm. long, at least twice as long as broad, 0.3–1.2 cm. wide, acute at apex, distinctly cuneate at base, the margins callose, distinctly so beneath, the teeth glandular, appressed, falcate, minute, 1–1.5 mm. apart, the costa prominent above and below, the secondary veins distinctly prominent above, evanescent, rarely distinct (if so, plane and blending with lamina), 1–1.5 mm. apart, spreading somewhat arcuately at a 60° angle from costa, the tertiary veins irregular-parallel to secondary veins and somewhat prominent above; stipules striate, linear-subulate, 4.5–5.5 mm. long, the cilia well-spaced, ascending at oblique angle, elongate, the middle ones 3.5–6.5 mm. long; flowers 1–3 per bostryx (often only one mature per bostryx) in axils of middle or apical leaves, the pedicels usually deflexed, slender, up to 2 cm. long, normally 2–3 times length of flower; sepals green-herbaceous, mostly equal, elliptic-lanceolate to subovate, 3.8–6 mm. long, acute at apex, usually with long terminal cilium subtended by shorter marginal cilia, the veins 4–8, prominent, strongly ascending, the margin entire or with red-glandular cilia; petals mostly obovate (or rarely broadly obovate-elliptic), up to 6 mm. long, usually longer than sepals at anthesis, tapering obtusely at apex, broadly or distinctly clawed beneath, the veins well-spaced, subflabellate, branching above middle; segments of exterior corona rarely absent, numerous in 1–3 continuous whorls, round to reniform-capitate, the filaments slender or somewhat expanded, 1–2 mm. long, up to one-half length of interior corona, the innermost the longest; segments of interior corona petaloid, free to base, oblong-obovate (rarely linear-obovate), 3–5 mm. long, rotund or truncate at apex, tapering toward base, the median prominence conspicuous and expanded at base, becoming ridge-like above, the veins oblique and mostly prominent; anthers oblong or linear-oblong, usually 2–2.5 mm. long (rarely up to 3.5 mm.), up to four-fifths length of interior corona, apiculate or vaguely retuse at apex, elongate-ovate or subrotund, 0.8–1.5 mm. long, tapering acutely or obtusely toward base of style, usually smooth, the three lobes conspicuous, the style subulate, 1.6–3.5 mm. long; capsule barely exceeding or distinctly exceeding sepals in length, 3.5–7 cm. long.

TYPE LOCALITY: Dominica, West Indies.

ILLUSTRATIONS: Aubl. Hist. Pl. Guian. **3**: *pl. 100*, as *S. adima*, 1775. Jacq. Sel. Stirp. Am. Hist. Pict. *pl. 77*. 1780. St. Hil. Mém. Mus. Hist. Nat. Paris **11**: 115, *pl. 6*, as *S. rubiginosa*, 1824. E. and P. Nat. Pfl. **3**. 6: 150. 1893.

DISTRIBUTION: Widely distributed through tropical America and the West Indies. Reported by numerous authors to be pantropical.

MEXICO[5]: Chinantla; *Galeotti 7177* (NY). GUATEMALA: Los Amates, *Bartlett 126* (NY). BRITISH HONDURAS: Yucatan Pen., *Gentle 1007* (NY). PORTO RICO: *Britton*

[5] As the collections of *S. erecta* have been so numerous, I have omitted the greater part of them.

and *Cowell 4079* (NY). HAITI: Dept. du Nord: Plaisance, *Leonard 9320* (NY). SANTO DOMINGO: Barrero, *Eggers 2044* (NY). GUADELOUPE: Camp Jacob, *Duss 2439* (NY). DOMINICA: Mantipo River, *Hodge 478* (NY). MARTINIQUE: Without locality: *Egler 294* (NY). ST. KITTS: Without locality, *Britton* and *Cowell 297* (NY). TRINIDAD: South of Dabadie, *Britton* and *Britton 2469* (NY). PANAMA: Bocas del Toro, Bocas Island, *Cooper 465* (F). FRENCH GUIANA: Cayenne; *Broadway 192, 535* (NY); *Leprieur* s. no. (NY). DUTCH GUIANA: Paramaribo, *Samuels 14* (NY). BRITISH GUIANA: Demarara River, *Anderson 153* (NY); Upper Mazuruni River, *De la Cruz 2071, 2084, 2187* (NY). VENEZUELA: Bolivar: Ciudad Bolivar, *L. H. Bailey* and *E. Z. Bailey 1663* (NY). COLOMBIA: Notre de Santander: Mesa de los Santos, 1400 m. alt., *Killip* and *A. C. Smith 20839* (NY); Huila: Neiva, *Rusby* and *Pennell 1062* (NY); Tolima: San Lorenzo, 800 m. alt., *Pennell 3535* (NY); El Cauca: Puerto de Buenaventura, *Triana* s. no. (NY), *2866* (!) (NY). PERU: Amazonas: Mouth of Rio Santiago, *Tessmann 4103* (NY); San Martin: Zepelacio, 1600 m. alt., *Klug 3404* (NY); Loreto: Pongo de Manseriche, *Killip* and *A. C. Smith 29134* (NY); *Iquitos, Tessmann 3647* (NY). BOLIVIA: Beni: Rurrenabaque, *Cardenas 1896* (NY); La Paz: Tipuani, 1400 m. alt., *Buchtien 5450* (NY); Santa Cruz: Yapacani River, *Kuntze* s. no. (NY). BRAZIL: Without locality, *Riedel* s. no. (NY); Amazonas: Rio Negro and Taquera, *Holt* and *Blake 563* (NY); Maranhão: *Snethlage 87* (F); Pernambuco: *Gardner 920* (NY); Bahia: Without locality, *Glocker 27* (NY); Matto Grosso: *Kuntze* s. no. (NY); Minas Geraës: Without locality, *Claussen 296* (NY); Rio de Janeiro: Without locality, *Martius 296* (NY); São Paulo: Without locality, *St. Hilaire 998* (!) (NY).

Common Names: "Herb of St. Martin," "Ironweed," and "Adima."

S. erecta, the type species of the genus, has the broadest geographical range of any American or West Indian species of the Ochnaceae. Its center of distribution appears to be in the West Indies, although I have not seen material from Cuba, apparently being replaced in this region by *S. brownei*. The leaves of the West Indian collections of *S. erecta* are usually large, the fascicles or bostryches are well spaced along at least the upper half of the stem, and the flowers are usually borne on elongate pedicels. Narrower leaf types with shorter pedicels and somewhat compressed bostryches are common throughout the Andean range of the species.

Although *S. erecta* shows definite relationships with *S. brownei*, particularly in the spacing of the bostryches along the stem, I have separated the former from the latter because of the differences in the structure of the staminodia of the two species.

4. **Sauvagesia grandifolia** Dwyer, sp. nov. Herba lignosa; petiolo 3–5 mm. longo; laminis foliorum chartaceis late ellipticis, 3.5–6 cm. longis, 1.0–1.9 cm. latis, apice acutis basi angusto-attenuatis margine serrato praeter base dentibus 1–3 mm. distantibus, costa utrimque subplana venibus principalibus secundariis 12–14 ascendentibus supra subprominentibus subter subplanis, 1–2.2 mm. distantibus, venis tertiariis subparallelibus arcuato-ascendentibus ad marginem in laxo reticulo dispositis; stipulis lineare-subulatis, 1–1.5 cm. longis, ciliis elongatis distantibus ramulosis basi margine gracile scariosoque; floribus 2–3 per bostrychem axillarem secundum longitudinem caulis dispositam pedicellibus 2 ± cm. longis; gemmis lineare-ovatis, 1 cm. longis, 3.1–3.5 mm. latis; sepalis aequalibus, lineare-lanceolatis aut lanceolatis, circ. 9 mm. longis, 2.7 mm. latis, basi obtusa apice acuminata margine

integro aut ciliis ascendentibus glandularibus apice cilio ad 9 mm. longo; petalis ellipticis apice triangularibus vénis flabellatis; coronae exterioris segmentis multis 2–3 seriatis filamentosis reniforme-capitatis vel rotundo-capitatis, 0.8–1.5 mm. longis segmentis coronae interioris oblongo-rectangularibus vel angusto-obovatis, 4.5–8 mm. longis, 1–1.7 mm. latis, apice truncatis erosisque medio jugo distincto venis flabellatis, antheris lineare-rectangularibus, 3–5 mm. longis, apice basique obtusis, filamentis teretibus, ad 0.5 mm. longis, ad 1.2 mm. latis, stylis triangularibus, ad 3 mm. longis, ad 1.2 mm. latis, stylis linearibus, ad 2.6 mm. longis; fructibus non visis.

TYPE LOCALITY: Petropolis, Rio de Janeiro, Brazil.

DISTRIBUTION: Known only from the type locality.

BRAZIL: Petropolis, Rio de Janeiro, *Glaziou 6478* (US, TYPE COLLECTION).

This species is obviously related to *S. erecta*, principally in the arrangement of the bostryches which are disposed along the length of the stem. Its very large chartaceous and elliptic leaves readily distinguish it from its ally.

5. SAUVAGESIA ELATA Bentham, London Jour. Bot. **4**: 107. 1842. Low shrubs up to 1 m. high, the stem thick, glandular, striate, usually somewhat prostrate at base; roots fibrous; petioles of leaves 3–5 mm. long; leaf-blades chartaceous, lanceolate, the middle ones usually 6–12 cm. long, 1.5–2.5 cm. wide, acuminate at apex, the margin not callose, the teeth minute, 2–4.5 mm. apart, the costa slender and prominent, indistinct above, the secondary veins slender, arcuate- and lax-ascending, scarcely prominent beneath, the reticulate areas distinct or indistinct; stipules appressed, elongate-deltoid, 1–1.5 cm. long, striate, the marginal cilia elongate, with or without smaller cilia at base; flowers 3–6 per bostryx, crowded in fascicles, the rachis slender 6–10 cm. above the uppermost leaves, mostly simple or bearing angular branches at base, the latter up to 6 cm. long, the pedicels 3.5–6.5 mm. long, the articulation-stalks 1.5–2 mm. long; sepals equal, lanceolate to ovate-lanceolate, about 6 mm. long, acute at apex, the apex terminating in a glandular cilium and rarely bearing glandular teeth; petals white, oblong, as long as or shorter than sepals, entire at apex, retuse, the notch bearing 1–3 glandular cilia, tapering little toward base, the veins numerous and pluriramose; segments of exterior corona numerous in 2–3 continuous whorls, the innermost whorl up to two-fifths the length of the interior corona, filamentous, the apices scarcely swollen; segments of interior corona obovate or oblong, up to 4 mm. long, the median ridge distinct, the veins prominent, well spaced and flabellate from ridge, the apex minutely retuse; stamens oblong or almost subulate, two-fifths the length of interior corona, the filaments short; ovary flask-shaped or simply ovate, the style short and crassate, tapering toward base, a little longer than ovary, the placentae extending up one-half the wall of ovary; capsule ovate-rotund, equal to sepals or rarely up to 4 mm. beyond apex of carpels, the latter scarcely rupturing to middle.

TYPE LOCALITY: British Guiana.

DISTRIBUTION: Known only from British Guiana.

BRITISH GUIANA: Waru-Waru Creek, Pomeroon River, *Bartlett 8142* (NY); Amakura, *De La Cruz 3472* (NY); Upper Mazaruni River, *De La Cruz 2286, 2828* (NY); Pomeroon River, *De La Cruz 2988* (NY), *2992* (NY), *3180* (NY); Kaieteur Falls, Potaro River, *De La Cruz 4456* (NY); Yarikita River, *Hitchcock 17652* (NY); Pomeroon District, *in Thurn 1941* (NY); Makauria River, *Sandwith 1569* (NY).

This species has the largest leaf-blades of the Sauvagesias; the lamina has distinctly arcuate-ascending veins, a character not present or not as obvious in the other species of the genus.

6. SAUVAGESIA RACEMOSA St. Hil. Mém. Mus. Hist. Nat. Paris **11**: 98. 1824. Woody herbs, 20–45 cm. high, simple or branching mostly at base, the branches canaliculate; petioles of leaves usually absent, rarely up to 3 mm. long; leaf-blades coriaceous, ascending, 0.5–1.5 cm. apart, oblong-lanceolate, up to 4 cm. long (2.5–3.5 cm. long in middle of stem), obtuse at apex, tapering obtusely or cuneately at base, the secondary veins numerous, 0.5–1.3 mm. apart, arcuate- and parallel-ascending, mostly subplane, the margin distinctly subcallose (especially beneath), the outermost dentiferous part narrow-alate (0.1 mm. wide), the teeth closely appressed and minute; stipules submembranaceous, striate, oblong-deltoid, up to 1.8 cm. long, the cilia elongate with small intermediate cilia along the scarious margin, the corpus basally and eccentrically fimbriate; flowers 1–5 in racemiform fascicular bostryches from the axils of reduced leaves, the fascicles 4–12 mm. apart, the rachis often branched at apex, 4–10 cm. above the uppermost leaves; flowers large, up to 13 mm. wide at anthesis; sepals ovate or oblong, about 5.5 mm. long, obtuse at base, the margins scarious, mostly entire, the veins ± 7, ascending and uniting acutely at apex; petals pink, obovate, 7–8.5 mm. long, subacuminate at apex, clawed or merely obtuse at base, the veins well spaced, flabellate, branching near margin; segments of exterior corona in a uniseriate or biseriate ring, the longest segments at least half the length of inner segments, subclavate at apex; segments of interior corona oblong, about same length as sepals, rotund at apex; anthers subsessile, oblong, 2.8–3.5 mm. long, obtuse at apex; ovary about 2 mm. long, the style subulate, up to 5 mm. long, more than twice the length of ovary, somewhat constricted at base; capsules turgid, ovate-triangular, 7–8.5 mm. long, about 4.5 mm. wide, exceeding sepals and segments of interior corona in length, the veins scarcely visible, the carpels purple-black when dry, the style rarely deciduous before dehiscence.

TYPE LOCALITY: Minas Geraës or São Paulo, Brazil.

ILLUSTRATION: St. Hil. Pl. Brés. **1**: *pl. 1, f. 1, 5.* 1824.

DISTRIBUTION: Apparently well distributed throughout Brazil, especially in the southern States.

BRAZIL: *Martius 1304* (NY); *Riedel* s. no. (NY); *Saint Hilaire 1188* (F, frag. of type (?) of *S. racemosa*); *Warming* s. no. (F, NY); Goyas: *Gardner 3009* (NY); Matto Grosso: Cuyabá, *G. D. Smith 332* (NY); Minas Geraës: Pirapora, *Burret, Brady* and *Mello 10153* (F); São Paulo: *Guilherme 173* (F); Ityrapina, *Guilherme 8329* (NY); Butantan, *Hoehne 784* (F). PARAGUAY: Without locality, *Jorgensen 4721* (F, NY).

7. SAUVAGESIA SPRENGELII St. Hil. in Bull. Soc. Philom. **2**: 173. 1823.

Sauvagesia erecta Aubl. Hist. Pl. Guian. Fr. **1**: 254. 1775. Not L.
Sauvagesia erecta Spreng. Neue. Entdeck. **1**: 296. 1820. Not L.
Sauvagesia serpyllifolia Mart. and Zucc. Nov. Gen. **1**: 37. 1824.
Sauvagesia fruticosa Mart. and Zucc. Nov. Gen. **1**: 38. 1824.
Sauvagesia kappleri Miq. Stirp. Surin. **7**: 105. 1851.
Sauvagesia rosacea Ule, Notizbl. Bot. Gart. Berlin **6**: 344. 1915.
Sauvagesia angustifolia Ule, Notizbl. Bot. Gart. Berlin **6**: 342. 1915.

Sauvagesia duckei Sleumer, Repert. Sp. Nov. 42: 263. 1937.
Sauvagesia striata Gleason and Dwyer, Brittonia 3: 169. 1939.

Woody herbs, up to 45 cm. high, ericoid in habit, the basal branches elongate, sharply ascending, the terminal branches somewhat angular and shorter; petioles of leaves up to 1 mm. long; leaf-blades coriaceous, striate, usually persisting at apices of branchlets, smaller leaves often aggregated in axils of larger leaves, the latter about 5.5 mm. apart, lanceolate to linear-lanceolate, up to 1.7 cm. long, rarely up to 2.5 cm. long, up to 0.6 cm. wide, acute at apex, obtuse at base, the margins subcallose and serrate, the costa prominent above and below, the secondary veins 6–7 per side, prominent above, oblique- or strongly ascending; stipules linear or linear-ovate, up to 7 mm. long, the cilia few, ascending, conspicuously 3-ciliate at apex; flowers 2–6 per bostryx, the rachis 2.5–6 cm. long, the bostryches well spaced, the pedicels slender, articulate, up 0.9 cm. long; sepals subequal or distinctly unequal, subpellucid, the outermost smaller, the inner lanceolate, up to 4.5 mm. long, obtuse to acute, eciliate or with a distinct terminal cilium, or the marginal cilia crowded near apex, obtuse at base, often with glandular areas (on outer surface) above the articulation-joint, the margins thin-scarious or scarcely differentiated, the cilia ascending, red-glandular, subulate, the veins 3–±7, branching obliquely and uniting acutely at apex, slender, flabellate; petals white to red, obovate to subcuneate, longer than sepals, obtuse to subcuneate at apex; segments of exterior corona usually numerous, in 2–3 continuous whorls or disposed as discrete fascicles, rarely few or completely absent, filamentous below, expanding into a reniform capitate or clavate apex, up to one-half length of interior corona; segments of interior corona oblong, 3–5 mm. long, 1.2–1.7 mm. wide, distinctly obtuse at apex, the vertical ridge distinct or subplane and tapering up to middle; anthers oblong, 1.3–2 mm. long, obtuse at apex, the filaments distinct, about 0.4 mm. long; ovary ovate or flask-shaped, 0.8–1.2 mm. long, the style subulate, at least twice length of ovary, constricted at base, often geniculate near apex; capsule linear-ovate, extending 2–2.5 mm. above largest sepals.

TYPE LOCALITY: British Guiana.

ILLUSTRATIONS: Mart. and Zucc. Nov. Gen. 1: *pl. 25, f. 1–9*, 1824. Velen. Vergl. Morphl. Pfl. *pl. 7* (fl. of *S. rosacea*), *f. 1–3*, 1910.

DISTRIBUTION: Known from Trinidad and apparently well distributed through tropical South America.

TRINIDAD: Aripo Savanna, *Britton* and *Britton 2926* (NY); Piarco Savanna, *Britton, Britton*, and *Hazen 61* (NY); Aripo Savanna, *Kuntze 1029* (NY). COLOMBIA: Rio Guatiquia, *Pennell 1638* (F, NY). PERU: Loreto: Tarapoto: *Spruce 4244* (NY); *Ule 6352* (F, photo of type of *S. rosacea*). FRENCH GUIANA: Without locality, *Leprieu 287* (F); Cayenne: *Leprieu* s. no. (F, NY); *Leprieu 231* (NY). DUTCH GUIANA: Forest of Zandery, *Samuels 264, 303* (NY). BRITISH GUIANA: Without locality, *Schomburgk 162* (NY); Ituni, Waruni Savanna, *Abrahams 45* (NY); Kaieteur Savanna, *Hollister* s. no. (NY); Essiquibo River, Kurupukari Savanna, *A. C. Smith 2172* (NY); Freschal (Mt. Roraima), *Tate 23* (NY). VENEZUELA: Kata, *Ule 8652* (F, photo and twig of type of *S. angustifolia*); Amazonas: Mt. Auyan-Tepui, *Tate 1312* (NY, type of *S. striata*). BRAZIL: Para: Vigia, *Drouet 2119* (F); Minas Geraës: Minas Gervis, Ilhoes, *Blanchet 1875* (F, NY, type collections of *S. serpyllifolia*).

This species exhibits much diversity in habit, thus accounting for its relatively large number of synonyms. It is well established in the sandy sa-

vannas, having a wide distribution through the eastern sections of north and central South America. The exterior corona, although rather uniform in shape, is frequently fasciculate or entirely absent. This condition suggests that the presence or absence of the segments of the exterior corona is not too reliable a character in the segregation of the species of *Sauvagesia*. *Spruce 4244* (NY) is noteworthy as its flowers invariably show the exterior corona reduced to a few segments. Although Sleumer's species, *S. duckei*, as ascertained from his description, has very large leaves, it cannot be segregated from *S. sprengelii* on the basis of the other characters enumerated.

8. SAUVAGESIA LONGIFOLIA Eichl. in Mart. Fl. Bras. **13**(1): 407. 1871. Woody herbs up to 70 cm. high; branches often basal, strongly ascending; leaf-blades subsessile, thin-coriaceous, strongly ascending, 0.8–1.3 cm. apart, linear-lanceolate, 3–9 cm. long, 0.5–0.9 cm. wide, distinctly acute at apex, narrow-attenuate at base, the margin serrate, the teeth minute, glandular, uncinate, the costa prominent above and below, the secondary veins numerous, prominent above, subplane beneath, irregular-ascending, spreading from costa at about 70° angle; stipules appressed, striate, linear, up to 1.5 cm. long, the cilia ascending, as long as or longer than corpus in length; flowers 1–3 in fascicular racemiform bostryches, the latter arising from the axils of reduced leaves, the rachis slender and terminal, up to 10 cm. above uppermost leaves, the fascicles 1–1.3 cm. apart; sepals subequal, striate, lanceolate to elliptic, ± 6 cm. long, acute at apex, terminating in a long glandular cilium about 2 mm. long, the margins entire or with small ascending, often uncinate teeth, the apical cilia of two sizes; petals obovate, up to 6 mm. long, subclawed at base, obtuse to subacute at apex, the veins flabellate; segments of exterior corona numerous, in 2–3 continuous whorls, reniform-capitate, up to 1.7 mm. long, about one-third length of interior corona; segments of interior corona oblong, up to 4.2 mm. long, obtuse or slightly retuse at apex, the median ridge distinct; anthers subsessile, up to 2.5 mm. long, about or a little more than one-half the length of segments of interior corona, obtuse at apex; ovary ovoid to conic-ovoid, 1–1.5 mm. long, the style awl-shaped, almost 3 times the length of ovary, constricted at base; capsule minutely granular, ovate-rotund, 5.5 mm. long, 3 mm. wide at base, tapering narrowly at apex, scarcely exceeding reflexed tips of persistent sepals (fig. 1, *a–j*).

TYPE LOCALITY: Cataract Caldnac, Brazil.

ILLUSTRATION: Eichl. in Mart. Fl. Bras. **13**(1): *pl. 83*. 1871.

DISTRIBUTION: Known from the Pacaraima Mts. on the British Guiana-Venezuela boundary, from French Guiana, and from Brazil.

BRITISH GUIANA—VENEZUELA BOUNDARY: Mt. Auyan-Tepui, 1100 m. alt., *Tate 1314* (NY). FRENCH GUIANA: Without locality, *Leprieu* s. no. (NY). BRAZIL: Without locality, *Sellow* s. no. (F, photo).

9. SAUVAGESIA AMOENA Ule, Notizbl. Bot. Gart. Berlin **6**: 341. 1915. Erect herbs up to 40 cm. high, branching at base; leaf-blades rigid, deflexed, subsessile, coriaceous, lustrous-green above, straw-colored beneath when dry, persisting along most of stem, crowded, ovate, ± 7 mm. long, 4 mm. wide, acute at apex, the costa conspicuous above and below, the secondary veins ± 10, arcuate-ascending, more conspicuous beneath, the tertiary veins con-

spicuous beneath, the margins callose with 6 minute ascending teeth; stipules linear-subulate, up to 5 mm. long, the margins subcallose with 5–7 divergent cilia as long as corpus; inflorescence terminal, paniculoid, the branches arising from most terminal leaves; flowers large, about 1 cm. wide at anthesis, 2–3 per bostryx, the fascicles 0.7–1 cm. long, the articulation-stalk 2 mm. long, the outermost bracts leaf-like, up to 3.7 mm. long, tapering toward apex; sepals unequal, ovate to ovate-lanceolate, 3–6 mm. long, erose at apex, bearing a semicircle of minute cilia on apical margin, the base on outer surface often with a yellow glandular area above articulation-joint, the margins scarious, entire or with ascending glandular cilia above middle; petals deep purple, subequal, inversely triangular, 6–8 mm. long, about 5 mm. wide, subrotund at apex, clawed at base, the veins flabellate; segments of exterior corona unequal, numerous, 3-seriate, reniform-capitate or anchor-shaped, 1.1–1.6 mm. long, up to one-fourth length of inner corona; segments of inner corona obovate-elongate, about 4.5 mm. long, united indistinctly at base into a cup, the median ridge of each segment prominent, broad below middle, becoming narrow toward apex, the veins prominent and ascending from ridge; stamens linear-elliptic, 1.5–3 mm. long, obtuse above, the filaments 0.2 mm. long, obtuse above; ovary ovate-rotund, the style about three times length of ovary; capsule narrow-ovate-lanceolate, equal to or exceeding sepals in length, acute at apex.

TYPE LOCALITY: Summit of Katá, Pacaraima Mts., British Guiana-Venezuela boundary.

DISTRIBUTION: Endemic to the Pacaraima Mts., British Guiana-Venezuela.

BRITISH GUIANA—VENEZUELA BOUNDARY: Mt. Auyan-Tepui, *Tate 1313* (NY); Summit of Katá, *Ule 8650* (F, photo of type of *S. amoena*).

S. amoena is a rare endemic species marked by its distinctly ovate and often deflexed leaves.

10. SAUVAGESIA RAMOSISSIMA Spruce ex Eichl. in Mart. Fl. Bras. **13**(1): 409. 1871. Slender woody herbs up to 30 cm. high; branches rubescent, angular, and patent at apex; leaf-blades subsessile, chartaceous, elliptic-lanceolate, up to 1.5 cm. long, 0.3–0.4 cm. wide, 0.5–0.8 mm. apart in middle of stem, acute at apex, cuneate at base, the secondary veins prominulous above, slender and not prominent beneath, the margin with small glandular teeth, distinctly narrow-callose beneath; stipules appressed, striate, linear, 3–5 mm. long, filamentous-ciliate; inflorescence paniculate, the rachis up to 8 cm. long, jointed or zig-zag, the flowers 3–6 per bostryx, the fascicles 0.7–1 cm. apart, distinctly pedunculate, the peduncles angular, slender, patent, ascending, 0.5–2 cm. long, becoming reduced in size toward apex of inflorescence, the pedicels capillaceous, 0.2 mm. wide, 2.5–10 mm. long, the articulation-stalks 0.7–4 mm. long, the bracts pectinose-ciliate, elliptic, up to 3 mm. long, fused with stipule at basal margin; flowers $\pm$ 2 mm. long at anthesis; sepals lanceolate, about 2 mm. long, acute at apex, terminating in a long glandular cilium; petals elongate-obovate, the same length as sepals, retuse at apex, the veins parallel-ascending; segments of exterior corona 1 to numerous, when numerous fasciculate, clavate, or only swollen at apex, up to one-third length of inner corona; segments of interior corona oblong, 1.5 mm. long, emarginate at apex, the ridge thin and median, the dorsal furrow

distinct, the veins flabellate and prominent; anthers oblong-lanceolate, about 0.7 mm. long, tapering acutely at apex, the filaments 0.3 mm. long; ovary ovate-oblong, as long as the awl-shaped style, the ovules few, glandular-verrucose, obovate; capsule ovate-conical, up to 4.5 mm. long, about twice length of sepals, obtuse at apex, the seeds reticulate, obovate, about 0.5 mm. long.

TYPE LOCALITY: Ribenirão, Matto Grosso, Brazil.

ILLUSTRATION: Eichl. in Mart. Fl. Bras. **13**(1): *pl. 82.* 1871.

DISTRIBUTION: Known only from the type locality, and from a Brazilian collection sans locality.

BRAZIL: Without locality, *Riedel* s. no. (NY).

This rare species is readily distinguished by its patent and paniculate inflorescence. Its peduncles and pedicels are more slender than those of any other woody species of the genus. According to Eichler the plant grows in a very moist habitat.

11. SAUVAGESIA DEFICIENS A. C. Smith, Lloydia **2**: 194. 1939. Shrubs about 30 cm. high; upper branches striate, the nodes below somewhat rough with remnants of stipules; roots fibrous; petioles of leaf-blades 1–2 mm. long, the leaf blades papyro-membranaceous, elliptic, 9–22 mm. long, 4–7 mm. wide, subcuneate at base, the margin callose, recurved, serrate, the costa subprominent above, prominent beneath, the secondary veins 6–8 on each side ascending; bostryches crowded at apices of branches, 2–4-flowered, arising from axils of uppermost leaf-blades, the pedicels slender, 3–6 mm. long; stipules lanceolate, 2–3 mm. long, the cilia elongate; sepals unequal, lanceolate, oblong-lanceolate, or rarely ovate, 2.7–5 mm. long, acute or somewhat obtuse at apices, the margin entire, glandular-erose at apex; petals white, obovate-rotund, 3–3.5 mm. long, the veins well spaced and flabellate; segments of exterior corona absent; segments of interior corona obovate-rotund, ± 3 mm. long, the margin entire or trilobed above, the veins serrate, arising from median part of swollen base of each segment; anthers oblong, 2 mm. long, subcordate at base, the filaments distinct; ovary ovate, 1.1–1.3 mm. long, distinctly 3-lobed, the style subulate, a little longer than ovary, somewhat crassate at base; fruit ovate, conical, up to 5.5 mm. long, the carpels almost twice length of sepals, acute, the median veins distinct.

TYPE LOCALITY: Mt. Iramaikpang, Kanuku Mts., British Guiana.

DISTRIBUTION: Known only from the type locality.

BRITISH GUIANA: Mt. Iramaikpang, 975 m. alt., Kanuku Mts., *A. C. Smith 3640* (NY, type of *S. deficiens*).

12. **Sauvagesia smithiana** Dwyer, sp. nov. Herba lignosa ad 30 cm. alta, ramulis multis valide ascendentibus caule glabra petiolis ad 4 mm. longis laminis chartaceis supra pallide viridis supra mediam caulem persistentibus, 6–12 mm. distantibus, lanceolatis, 1–2.7 cm. longis, 6.5–9 mm. latis, apice acutis costa utimque prominente ad basim expandente nervis secundariis 7–10 utrimque prominentibus subtus colore distinctis, margine utroque dentibus 6–10 uncinatis utroque cum minorem dentem sinu ferente, stipulis ad basim persistentibus linearibus, ad 8 mm. longis, apice constrictis ciliis elongatis apice 3-ciliatis, inflorescentia racemiforme rhachidibus ad 8 cm.

longis, bostrychibus in axillaribus minutorum foliorum pedicellis gracilibus, 4–6.5 mm. longis, articulo saepe a basi pedicelli ad 2.5 mm. longis, floribus sub anthesi circiter 7 mm. latis, sepalis aequalibus lanceolatis vel oblongo-lanceolatis, circiter 4 mm. longis, apice acutis margine integro vel dentibus parvis ascendentibus venis lateralibus ± 7 conspicuis prominentibusque, petalis brevioribus sepalis obovato-rotundis, 3–3.5 mm. longis, venis distantibus gracilibus vix flabellatisque, segmentis coronae exterioris desinentibus, segmentis coronae interioris pellucidis rotundis vel subrotundisque, 2.5 mm. longis, venis planis ± 3 oblique a basi ortis ad apicem vix flabellatis ramosisque, antheris oblongis segmentis interioris coronae brevioribus utroque anthero segmenti margine incluso, circiter 1.6 mm. longis, obtusis apice saepe retusis, filamentis 0.3–0.5 mm. longis, ovariis ovatis circiter 1 mm. longis stylis subulatis, 1.8 mm. longis, ovulis paucis ascendentibus, capsulis ovato-conicis, ad 6.5 mm. longis, 1–1.8 mm. super sepalis extendentibus (fig. 1, *k*, *m*).

TYPE LOCALITY: Mt. Roraima, British Guiana-Venezuela boundary line.

DISTRIBUTION: Known only from the type locality.

BRITISH GUIANA—VENEZUELA BOUNDARY: Mt. Roraima, 1500 m. alt., *Tate 321* (NY, type of *S. smithiana*).

The author has named this species in honor of Dr. A. C. Smith who assisted him so materially in the preparation of this paper.

S. smithiana and *S. deficiens*, two endemic species are closely related; the subrotund segments of their inner coronas are unlike those of any other species of *Sauvagesia*. The two species differ in the shape, size, and length of their stipules, in the morphology and venation of the segments of the inner corona, and in the relative size of their sepals. Unlike those of *S. smithiana* the leaf margins of *S. deficiens* are distinctly recurved.

13. SAUVAGESIA LINEARIFOLIA St. Hil. Mém. Mus. Hist. Nat. Paris **11**: 106. 1824.

Sauvagesia pusilla Mart. and Zucc. Nov. Gen. 1: 35. 1824.

Woody herbs up to 15 cm. high; branches of stem few to many, nodes swollen; leaf-blades persistent above, plane, subcoriaceous, 1.5–2.5 mm. apart, ascending, linear, up to 11 mm. long, 0.5 mm. wide, acute at apex, obtuse at base, the margin callose, the teeth well spaced and acuminate, the costa prominent above and below, the secondary veins inconspicuous; stipules linear, longer than nodes, the cilia strongly ascending and in a whorl of 3 at apex; sepals equal, lanceolate, about 1 mm. long, the margin entire or with ascending, appressed, and glandular cilia, the apex terminating in a stout cilium subtended by elongate marginal cilia, the veins 5–7 and prominent; petals ellipitic-rotund to obdeltoid, 3–4.6 mm. long, acute at base, the veins flabellate and slender; segments of exterior corona 5–10, 1–2 alternate with each segment of inner corona and up to one-half length of latter; segments of interior corona elliptic, 1.8–2.3 mm. long, the median vein distinct and not conspicuously ridge-like; anthers narrow-ovate, about same length as segments of interior corona, subrostrate at apex, the filaments almost as long as anthers; ovaries subrotund, up to 2.5 mm. long, the styles crassate, a little

longer than ovary, somewhat constricted at base; capsule exceeding sepals in length, the seeds oblong-rotund, about 1 mm. long.

TYPE LOCALITY: Servico do Rio Pardo, Minas Geraës, Brazil.

ILLUSTRATION: St. Hil. Mém. Mus. Hist. Nat. Paris **11**: *pl. 2, f. 1–8*, 1824.

DISTRIBUTION: Known from Venezuela and Brazil.

VENEZUELA: Amazonas: Rio Guainia and Rio Negro at mouth of Rio Casiquiari, *Spruce 3513* (NY). BRAZIL: Without locality, *Riedel* s. no. (NY); Goyas: *Gardner 3007* (F. NY); Minas Geraës: Servico do Rio Pardo, 1000 m. alt., *St. Hilaire* (F, photo of type of *S. linearifolia*).

14. SAUVAGESIA DEFLEXIFOLIA Gardn. Hook. Ic. **5**(1): *pl. 484.* 1842. Woody herbs, erect and slender, up to 70 cm. high; roots fibrous; branches of stem apical, angular, 1–2 mm. wide at base; leaf-blades sessile, deflexed, the proximal part of lamina appressed to stem, coriaceous, narrowly linear-elliptic or ovate-elliptic, ± 8 mm. long, about 1.3 mm. wide, strongly acuminate and terminating in a stiff cilium or simply with a small obtuse gland at apex, obtuse at base, the secondary veins scarcely visible above, strongly ascending, the tertiary veins slender and parallel, the margins callose, the teeth well spaced, falcate, about 0.5 mm. long; stipules appressed, subulate, 1.3–2 mm. long, the cilia slender, oblique-ascending; flowers 2–5, terminal, not in bostryches but solitary in axils of somewhat reduced apical leaves, about 6 mm. long at anthesis, the pedicels slender, up to 4 mm. long, often obscured by leaf-blades, the flowers seemingly sessile; sepals lanceolate, rarely broadly ovate, up to 4.7 mm. long, subclawed at base, obtuse above, the veins flabellate-ascending; petals white, obovate, about 4.5 mm. long, 3.5 mm. wide, the margins entire below, minutely toothed at apex, the median teeth more distinct; segments of exterior corona filamentous below, plane and lanceolate at apex, up to 1.8 mm. long, up to three-quarters the length of interior corona, transparent, oblong (or subovate), up to 3.7 mm. long, shorter than stamens, acute at apex, the median vein not conspicuously ridge-like, the lateral veins prominent, oblique-ascending; anthers linear-ovate, abruptly apiculate, 1–1.5 mm. long, the filaments 0.7–1.2 mm. long, the stamens about twice length of interior corona; ovaries smooth, distinctly 3-lobed, about 1.3 mm. long, the style crassate, subulate, somewhat constricted at base; capsules striate, elliptic before dehiscence, as much as 1.5 mm. beyond apex of sepals, the carpels acute, somewhat deflexed at dehiscence.

TYPE LOCALITY: Goyas, Brazil.

ILLUSTRATION: Gardn. Hook. Ic. **5**(1): *pl. 484.* 1842.

DISTRIBUTION: Known from a few collections in Venezuela, Colombia, Bolivia, and Brazil.

VENEZUELA: Amazonas: Esmeralda, alt. 100 m., *Tate 265* (NY). COLOMBIA: Boyaca: Oracue, *Haught 2707* (US). BOLIVIA: La Paz: Ixiamas, 250 m. alt., *Cardenas 2020* (NY). BRAZIL: Without locality, *Pohl 1263* (F).

As the specific name indicates *S. deflexifolia* is readily distinguished by its deflexed leaf-blades; although this character is found in one other member of the genus *S. amoena*, the two species are readily separated on the basis of floral characters. *S. linearifolia* is undoubtedly most closely related to *S. deflexifolia*, both species having linear stiff leaf-blades, ovoid anthers with

long filaments, and crassate styles. The fact that the flowers are not fascicled but solitary is suggestive of *S. imthurniana;* however, the flowers of the latter are disposed on peduncles.

It is worthy of note that *S. deflexifolia,* considering its wide geographical distribution in tropical America, has been little collected.

15. SAUVAGESIA PULCHELLA Seem. Bot. Voy. Herald **1**: 80. 1852. Small herbs, 5–15 cm. high; branches of stem slender, short, the lowermost usually 3–5 cm. from base of stem, arcuate or angular-ascending; leaf-blades usually persisting below middle of stem, subsessile, well spaced, chartaceous, elliptic, about 17 mm. long, 2–4 mm. wide, acute at apex, cuneate at base, the lamina narrow-alate on the very short petiole, the costa prominent above and below, scarcely distinguishable from lamina below, the secondary veins prominent, parallel-ascending; stipules striate, linear- or elliptic-falcate, up to 6 mm. long, the elongate cilia of corpus each with a distinct lateral and median gland; flowers 2–5 per bostryx, fasciculate in uppermost leaf-blades, the pedicels up to 5 mm. long, the articulation-stalks about 1 mm. long, the bracts linear or lanceolate, the margins serrate, ciliate toward base, the cilia not glandular-jointed; sepals equal, lanceolate, 1.5–2.7 mm. long, acute, the margins entire except for a few short cilia toward apex, with or without a distinct terminal cilium, the veins ± 3; petals elliptic, 1.8 mm. long, tapering gradually above middle, rotund at apex, the veins 3, parallel-ascending; exterior corona absent; segments of interior corona oblong, about 1.5 mm. long, the veins usually parallel-ascending, the median veins more conspicuous and branching freely above middle; anthers subrotund or ovate, about 0.4 mm. long, obtuse or acuminate at apex, seemingly bidentate at apex at dehiscence, the filaments slender, about 0.5 mm. long; ovaries ovate, 0.8–1.5 mm. long, the style short, thick, about 0.5 mm. long; capsule narrow-ovate, almost twice length of sepals.

TYPE LOCALITY: Savannas of Panama.

DISTRIBUTION: Widely distributed through the high savannas of northern South America.

COLOMBIA: El Cauca: Alt. San Francisco, *Andre 2853* (F, NY); Tocota, 1500–1800 m. alt., *Lehman 8965* (NY); Magdalena: Santa Marta near Jeracasea, 1000 m. alt., *H. H. Smith 557* (F, NY). VENEZUELA: Aragua, 760 m. alt., *Llewelyn Williams 10814* (F). BRAZIL: Without locality, *Burchell 6960* (NY).

Although Seemann in his original description of *S. pulchella* notes that it is common in the savannas of Panama, I have not seen additional collections from that area.

16. SAUVAGESIA TENELLA Lam. Ill. **2**: 119. 1793.

Sauvagesia nana Ule, Notizbl. Bot. Gart. Berlin **6**: 345. 1915.
Sauvagesia gracilis Ule, Notizbl. Gart. Berlin **6**: 345. 1915.
Sauvagesia inconspicua Dwyer, Lloydia **2**: 195. 1939.

Herbs 3–7 cm. high, simple or rarely with apical or basal branches, the stem glandular-smooth, seemingly ribbed; leaf-blades glandular-carnose, sessile, elliptic, 3–8 mm. long, 1.8–3 mm. wide, subacute to obtuse at apex, subcuneate at base, the margins with minute cilia or rarely entire, the secondary veins immersed and evanescent; stipules linear, 1–3 mm. long, the cilia 5–7,

well-spaced and exceeding corpus in length; flowers usually 3 per bostryx, the fascicles 1–2, terminal, subtended by reduced stipulate leaves, the pedicels slender, 6–7 mm. long; sepals herbaceous-green, lanceolate to ovate, 3.2–4 mm. long, setose-aristate at apex, the margins mostly scarious, the veins 3+, ascending; petals pink or white, obovate, 3–5 mm. long, equal to or exceeding sepals in length, usually distinctly clawed at base, the veins evanescent and flabellate; segments of exterior corona absent; segments of interior corona usually oblong, rarely narrow-obovate, usually slightly shorter than stamens, rounded or flat-obtuse at apex, the median ridge not obvious, the dorsal furrow absent, the veins 1–2, ascending, usually branching at middle or above; stamens usually exceeding segments of interior corona in length, up to 2 mm. long, the anthers oblong, obtuse at apex, the filaments shorter or longer than anthers; pistil 1–1.5 mm. long, the ovary ellipsoid or rotund, the style shorter than ovary; capsule equal to or exceeding sepals in length, mostly turgid at base (fig. 1, *n–p*).

TYPE LOCALITY: Tropical America.

ILLUSTRATION: St. Hil. Mém. Mus. Hist. Nat. Paris **11**: *pl. 1. B, f. 1–7*, 1824.

DISTRIBUTION: Widely distributed through the savannas of Cuba, Central America, and tropical South America.

CUBA: Cienequita?, *Combs 439* (NY); Oriente: Sabana San Felipe, *Ekman 2398* (NY); Santa Clara: Manacas, *Leon* and *Cazanas 5907* (NY); Without locality, *Wright 2131* (NY). GUATEMALA: Narbasco, *Bernoulli 947* (NY). PANAMA: Coclé: *Allen 830* (NY); Pacora and Chepo, *Woodson, Allen,* and *Seibert 1657* (NY). BRITISH GUIANA: Wichabai, Rupununi River, *A. C. Smith 2309* (NY, type of *S. inconspicua*). BOLIVIA: La Paz: S. Marcos and Rio Branco, *Ule 7880* (F, photo of type of *S. nana*); Rio Branco, *Ule 8119* (F, photo of type *S. gracilis*).

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A NEW SECTION MICROPHYLLAE IN AGROSTIS

ALAN A. BEETLE

In mentally picturing the genus *Agrostis* (Gramineae) it is easy to fall into the habit of thinking of the glumes as awnless. Shishkin (1934) in keying out of 29 species in the Russian flora definitely states for all "glumes always without awn." The glumes of our commonest American species are awnless. It is then somewhat disconcerting to come upon *A. exarata* Trin. and find that, although the glumes of the typical form are only acute, specimens treated as var. *monolepis* may have glumes rather long-awned (1 mm. or more). To this author's knowledge the only other currently recognized species in *Agrostis* described as bearing an awned glume is *A. hendersonii* Hitchc. The following investigation was undertaken to determine whether there were more than varietal significance to the awned-glumed plants usually placed under *A. exarata* and what could be the position in *Agrostis* of such unusual species, the thought being that they might better fall in *Polypogon* where awned glumes are usual.

The type locality of *Agrostis exarata* (Trin. Gram. Unifl. 207. 1824) is Unalaska, where it was collected by Eschscholtz. The latest treatment of Alaskan *A. exarata* (Anderson 1944) gives a description that agrees with those of Scribner and Merrill (1910), the original description, and Trinius' illustration in *Species Graminicum,* vol. 1 (1928). It also agrees with the characters of the widest-ranging segregate of the *A. exarata* complex in North America, which always has been considered, and apparently correctly so, as typical *A. exarata.* Specimens have been collected, according to Hitchcock (1935, 1937) from "Western Nebraska, to Alberta and Alaska, and southward to New Mexico, California, and Mexico." The map 683 in the Hitchcock *Manual* omits a dot for South Dakota, apparently overlooking the report by Rydberg (1896) of its rare occurrence in the Black Hills. This record has recently been reaffirmed by *Ester Suter 10,* Wind Cave Canyon, Custer County, South Dakota, collected in 1936.

Typically, then, *A. exarata* is a perennial with an awnless lemma (rarely awned and then the awn short and not bent), a prominent palea usually half the length of the lemma, scabrous glumes which are acute but not attenuate, and a narrow slender panicle, the ascending appressed branches floriferous to the base. These characters are well demonstrated in the following collections taken at scattered points throughout the range: TEXAS: *Moore & Steyermark 3158.* ARIZONA: *Thornber 492.* UTAH: *Stanton 590.* NEVADA: *Kennedy 4068.* CALIFORNIA: *Beetle 3028.* OREGON: *Heller 13056.* WASHING-

TON: *A. A. & E. G. Heller 4018*. BRITISH COLUMBIA: *Eastham 9039*. In California this species is commonly found at higher elevations, in the northern counties and southward both in the Coast Ranges and the Sierra Nevada to the mountain peaks of the southern counties.

Agrostis exarata has not lived up to the suggestion of promise indicated in many early publications of the United States Dept. of Agriculture (Tracy & Nealley 1888, Anderson 1889, Vasey 1889, Scribner 1900, Forest Service 1914). The plate 13 of Tracy & Nealley (which is the same as plate 49 of Vasey) is an excellent illustration of typical *A. exarata* and agrees in all details with the plate of Trinius mentioned above. The plate 106 of Vasey listed as *A. exarata* var. *pacifica* is also good *A. exarata* differing only in the short, unbent, included awn, a sporadically occurring remnant of what was apparently formerly an awned condition or else representing a visible trace of an awned parentage somewhere in the ancestry. Water is too strong a limiting factor in the life history of *A. exarata* to make it more than an ephemeral plant on most of the western range. Failure of the grass when sown on the open range has been reported by Lyon and Hitchcock (1904).

Two California species are closely related to *A. exarata:* the first *A. rossae* Vasey of higher elevations, a dwarf, tufted plant with narrow, crowded basal leaves and awnless lemma; the second, *A. californica* Trin., of coastal bluffs where it is easily marked by its dense, broad panicle and strongly scabrous glumes. These three species probably belong to the section *Trichodium* Michx. of *Agrostis*. For a clearer picture a sectional treatment of *Agrostis* as a whole is needed.

On the other hand the material treated by Hitchcock (1935, 1937) as varieties *monolepis* and *ampla* of *A. exarata* and as *A. hendersonii* differ in a number of respects and are here considered to comprise a separate section, *Microphyllae*, consisting of four species with varieties. From all other species of *Agrostis* this section is separated by the awning of the glumes. From *Agrostis exarata* and relatives, with which they have usually been confused though they are not necessarily closely related, they are separated as follows:

Section *Microphyllae*	*A. exarata, A. rossae,* and *A. californica*
(1) Glumes attenuate-tipped or awn-tipped.	(1) Glumes acute.
(2) Lemma with a bent, exserted awn (figs. 1, 2, 6, 7, 8).	(2) Lemma awnless, or with a short, unbent, included awn (figs. 3, 4, 5).
(3) Palea absent or obsolete.	(3) Palea present and prominent.

The chromosome number of typical *A. exarata* Trin. as reported by Nielsen (1939), is $2n = 28$. The chromosome number of *A. ampla* Hitchc. (*Stebbins 2816, 2953*) of Sect. *Microphyllae* is $2n = 42$ (Stebbins & Love 1941), thus supplying cytological evidence that two specific entities may be involved. Through the kindness of Dr. G. L. Stebbins, Jr. (College of Agri-

culture, University of California) the chromosome number of *A. hendersonii* Hitchc. (*A. microphylla* var. *hendersonii* of this paper) may be reported as $2n = 42$. The count was made from material grown in Shasta County, California (*Beetle & Stebbins 3354*).

Section **Microphyllae** Beetle, sect. nova.

Glumis scabris ad dorso, aristatis; lemmis arista prominenti geniculata exserta munitis; palea nulla.

Two short-lived perennials and two annuals along the Pacific coast of North America.

KEY TO THE SPECIES

Glumes 2.75–3 mm. long; lemma 1.5 mm. long; the awn 3 mm. long, bent at the middle. 1. *A. ampla.*

Glumes 3–6 mm. long; lemma 2–4 mm. long, the awn 3.5–10 mm. long, bent below the middle.

Stout perennials of moist meadows; panicle open, 1–2 dm. long; basal leaves broad and conspicuous. 2. *A. inflata.*

Slender annuals of vernal pools; panicle dense, up to 7 cm. long; basal leaves few and ephemeral.

Lemmas, if pubescent at all, only tufted at base; lemma only shortly toothed at apex.

Glumes 3–4 mm. long; lemma 2 mm. long, the awn 3.5–4 mm. long. 3. *A. microphylla.*

Glumes 4–6 mm. long; lemma 3 mm. long, the awn 7 mm. long. 4. *A. microphylla* var. *intermedia.*

Glumes 7–8 mm. long; lemma 4 mm. long, the awn 10 mm. long. 5. *A. microphylla* var. *hendersonii.*

Lemmas evenly pubescent over the back; lemma deeply two lobed, the lobes with setaceous teeth 1 mm. long. 6. *A. kennedyana.*

1. AGROSTIS AMPLA Hitchc. U. S. Dep. Agr. Bur. Pl. Ind. Bull. **68**: 38. *pl. 20.* 1905.

Tufted perennial; culms one to many, erect (or somewhat geniculate from the lowest node), up to 6 dm. tall; depending on the habitat the blades mostly basal, or evenly scattered on the culm; blades up to 5 mm. broad, scabrous on the margins and minutely scaberulous on the nerves; panicle typically well-exserted from the upper sheath, about 1 dm. long, the lowest fascicle (ca. 1 cm. long) somewhat remote, the other fascicles about equal and appressed to form a dense panicle; glumes subequal, 2.75–3 mm. long, including the awn (usually ca. 1 mm. long, occasionally prolonged or absent) scaberulous on the midrib and minutely so on the back; lemmas ca. 1.5–2 mm. long, long-awned from a deeply bifid apex, smooth, the callus with two tiny tufts of white hair; awn ca. 3 mm. long, once geniculate at about the middle; palea absent or obsolete; anthers 0.33 mm. long; caryopsis brown, 1 mm. long. (fig. 1.)

TYPE LOCALITY: Oregon, Multnomah County, Rooster Rock, *Suksdorf 135.*

DISTRIBUTION: Washington and Idaho south to California.

WASHINGTON: Clallam Co., Olympic Mts., *A. D. E. Elmer 1953;* Chelhalis Co., Montesano, *A. A. & E. G. Heller 4010.* IDAHO: Elmore Co., Atlanta, *Christ & Ward 8326.*

OREGON: Yamhill Co., McMinnville, *Shear 1633, 1643, 1646, 1650;* Oregon City, *Chase 4955;* Klamath Falls, *Hitchcock 2979.* CALIFORNIA: Humboldt Co., *Tracy 4825, 1754;* Sonoma Co., *Yates 6582;* Tulare Co., *Wiggins & Ferris 2656;* Santa Cruz Co., *Howell 19598.*

The names *Agrostis microphylla* Steud. and *A. inflata* Beal are applied to species whose descriptions follow. Discarding the invalid *Agraulus brevifolius* Nees (1857), the next specific name is *Polypogon alopecuroides* Buckl. (1863) which, though validly published, cannot be transferred to *Agrostis* because of the earlier *A. alopecuroides* Lam. (1791). The next name then, is *Agrostis ampla* Hitchc. (1905) which was carefully described and illustrated (see his plate 20). The description and illustration fit the plants which have long passed as an awned variety of *A. exarata* in all but one detail. Hitchcock states that the glumes are "acuminate, but not awn-pointed." Many specimens that fall into this group on all other characters have glumes that are prominently awned. Because of the differences in technical measurements, the usually awned glumes, the minute or absent palea, and the awned lemma, *A. ampla* Hitchc. is taken to represent a distinct species.

The very dense-panicled forms (represented by *Beetle 2890, Stebbins 2958, Tracy 14016,* and *Shear 1650*) are sporadically occurring and only represent a form which may be treated as: *Agrostis ampla* Hitchc. f. **monolepis** (Torr.) Beetle, comb. nov. [*Polypogon monspeliensis* var. *monolepis* Torr. U. S. Rept. Expl. Miss. Pacif. **5**: 366. 1857. *Agrostis exarata* var. *monolepis* (Torr.) Hitchc. Am. Jour. Bot. **21**: 136. 1934.]

2. AGROSTIS INFLATA Beal, Grasses N. Am. **2**: 325. 1896.

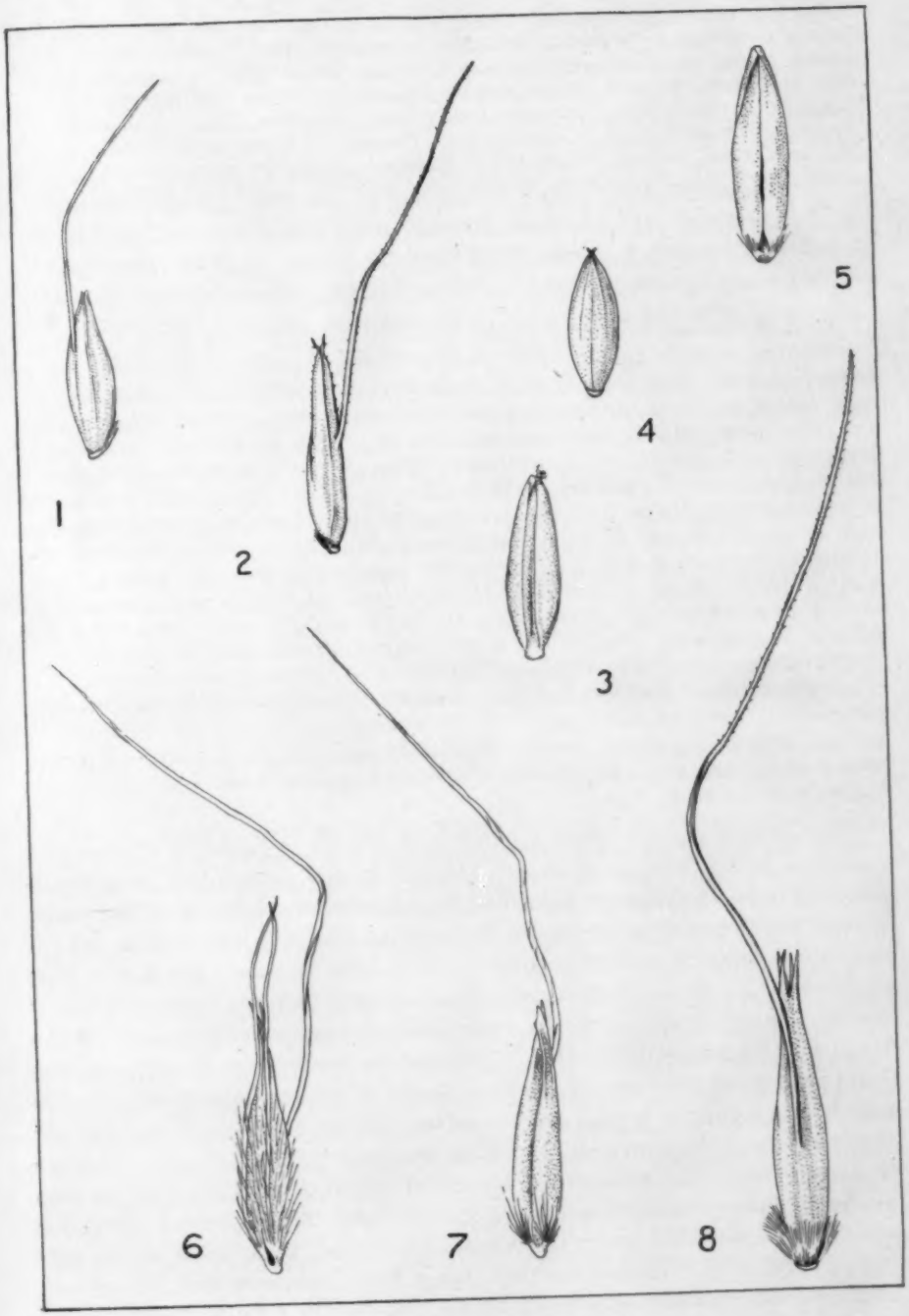
Perennial, culms clumped, strictly erect, 5–8 dm. tall; leaves sometimes crowded at the base, basal and culm leaves up to 8 mm. broad, 1–1.5 dm. long, scabrous on the nerves and margins; panicle 1–2 dm. long, often diffuse, the pedicels not always floriferous to the base; awned glumes 4–5 mm. long, scabrous on the midrib; lemma 2 mm. long, glabrous except for two small tufts at the base, the awn 6 mm. long, geniculate below the middle; palea absent. (fig. 2.)

TYPE LOCALITY: Vancouver Island, British Columbia, *Macoun 258.*

DISTRIBUTION: Boggy meadows, coast ranges at low elevations, Vancouver Island, British Columbia south to southern California.

Explanation of figures 1–8.

Sample undissected florets of *Agrostis* species, mainly showing the lemma. FIG. 1. *A. ampla,* drawn from *Tracy 14016.* FIG. 2. *A. inflata,* drawn from Mendocino County, Calif., material collected by *P. B. Kennedy,* May 30, 1929. The sheet is marked in Hitchcock's handwriting "*Agrostis exarata microphylla* (Steud.) Hitchc." and "differs from others in having slender diffuse panicle." FIG. 3. *A. rossae,* drawn from *Baker 10694.* FIG. 4. *A. exarata,* drawn from California material. FIG. 5. *A. californica,* drawn from *Pringle 12.* FIG. 6. *A. kennedyana,* drawn from the type. FIG. 7. *A. microphylla* var. *intermedia,* drawn from the type. FIG. 8. *A. microphylla* var. *hendersonii,* drawn from *Beetle 3277.* The figures drawn by Viola Memmler and Margery P. Mann.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BRITISH COLUMBIA: Vancouver Island, *Macoun* in 1887 (the same as the *Macoun 82* reported by Hitchcock in 1905 as *A. ampla*), *Dawson* in 1885, *Hitchcock 4875*. WASHINGTON: Kitsap Co., *Otis 1644*. OREGON: Polk Co., *Ferris 7790;* Roseberg, *Howell* in 1887; Marshfield, *Haydon*. CALIFORNIA: Del Norte Co., *Yates 5750* and *Davy 5950a;* Humboldt Co., *Tracy 3785, 8271, 8285, 12809,* and *13857;* Mendocino Co., *Davy & Blasdale 5199, 5262, 5299, Beetle & Stebbins 3499;* Sonoma Co., *Wagnon 190, 214, Yates 5574, 6565, 6582;* Santa Cruz Co., *Howell 19600;* Marin Co., *Davy 4337;* Monterey Co., *Kennedy* in 1928, *Davy 7506, Heller 6828;* Orange Co., e. of Santa Ana, *Love* in 1942.

The plants of *Agrostis inflata* are in some ways intermediate between *A. microphylla* and *A. ampla*. They have the longer awn and larger glumes of the former but the perennial habit and longer inflorescence of the latter.

3. AGROSTIS MICROPHYLLA Steud. Syn. Pl. Gram. **1**: 164. 1854.

Annual, loosely tufted, with slender, fibrous roots; culms erect, often branched at the base, slender, smooth, constricted at the black nodes, 1–4 dm. tall; leaves of the culm 2 or 3; sheaths nearly smooth, closed, shorter than the internodes; blades erect, scabrid, flat or loosely involute, 2–5 cm. long; ligule usually lacerate, 2–4 mm. long; inflorescence a close-flowered, spike-like panicle, up to 7 cm. long, light green or purplish, the numerous exserted awns usually giving it a feathery appearance; rays in semiverticillate clusters at the 5–7 nodes, unequal, barely exceeding the intervals, floriferous to the base; glumes 3–4 mm. long, subequal, scabrous on the keel; lemma 2 mm. long, broadly oblong, 4-toothed at the apex, smooth except at the base, thin, obscurely 4-nerved, the awn arising above the middle, geniculate below the middle, hispidulous, slender, 3.5–4 mm. long; palea absent.

TYPE LOCALITY: "in Am. Sptr.," *Douglas*.

DISTRIBUTION: California Coast Ranges, Humboldt Co. south to San Diego Co.

Humboldt Co., *Heller 13772* and *Tracy 13857;* Sonoma Co., *Yates 6550;* Marin Co., *Howell 19479;* San Mateo Co., *Abrams 2458;* San Diego Co., *Orcutt 1176;* and Drews Valley, *Austin & Bruce 1740*.

The earliest specific name applied to a species included in the present section is *A. microphylla* Steud. (1854). Only two years after its original publication in 1856 Torrey identified the name with specimens of *A. ampla* Hitchc. which was then an undescribed species. The application of *A. microphylla* was certainly correctly established in 1893 by Vasey and beautifully illustrated. The plant shown agrees in all respects with the original description of Steudel. Vasey correctly observes in reference to Bolander (1864–1865) and Thurber (1880) that "This species has been referred to *A. exarata*, as it resembles some of the small forms of that variable species, but it may be distinguished by the smaller leaves, slender culms, and long awns." However, the species has continued to be confused with *A. exarata* (and later *A. ampla*) under the influence of Hitchcock (1905, 1912, 1935, 1937) whose too broad interpretation has crossed specific lines. The following specimens which have been cited under *A. microphylla* Steud. are typical of the species: *Orcutt 1176* (Hitchcock 1912), *Davy 5142* (Scribner 1901, Hitchcock 1905), and *Davy 6573* (Hitchcock 1905).

4. A. MICROPHYLLA var. **intermedia** Beetle, var. nov.

Agrostidi microphyllae affinis sed glumis aristatis 4–6 mm. longis, lemma 3 mm. longa arista 7 mm. longa munita recedit. (fig. 7.)

TYPE LOCALITY: California, Lake County, 2.9 miles north of Middletown, May 11, 1943, *J. T. Howell 18063* (TYPE in the Agronomy Division Grass Herbarium, Univ. of California, Davis, Calif.).

DISTRIBUTION: California, lower elevations away from the coast.

Lake Co., (see type) *Eastwood & Howell 5642;* Napa Co., *Tracy 1856;* Calaveras Co., *Carlson 302, Yates 162;* Merced Co., *Hoover 532a* (reported as *A. hendersonii* by Hoover, 1936).

5. A. MICROPHYLLA var. **hendersonii** (Hitchc.) Beetle, comb. nov.

A. hendersonii Hitchc. Jour. Wash. Acad. **20**: 381. 1930.

Like typical *A. microphylla* and the var. *intermedia* except for the following measurements: awned glumes 7–8 mm. long, lemma 4 mm. long, conspicuously tufted at the base; awn of the lemma 10 mm. long. (fig. 8.)

TYPE LOCALITY: Oregon, Jackson County, Sams Valley, near Gold Hill, *Henderson 12387.*

DISTRIBUTION: vernal pools, inland, Oregon (type locality) and California.

CALIFORNIA: Shasta Co., *Beetle 3277* (cited in Beetle 1943), *Beetle & Stebbins 3354;* Calaveras Co., *Yates 5162, Carlson 300, 950.*

6. **A. kennedyana** Beetle, sp. nov.

Agrostidis microphyllae habitu; culmis ad 2 dm. altis; panicula densa, 1–4 cm. long; glumis imparibus, prima 4 mm. longa, altera 3 mm. longa, callo prominenti; lemma profundissime bifida, aequaliter pubescenti, corpore 1.5–2 mm. longo, lobis dentibus setaceis ca. 1 mm. longis munitis, arista 5–6 mm. longa geniculata e dorso exorienti; palea nulla; caryopsidi 1–1.5 mm. longa. (fig. 6.)

TYPE LOCALITY: California, San Diego County, San Diego, April, 1902, *G. B. Grant 896* (TYPE in the herbarium of the Univ. of California, Berkeley). Only other collection seen: Calif., San Diego Co., La Jolla, May 3, 1914, *F. E. & E. S. Clements 292* (distributed as *Gastridium lendigerum*).

Named for Patrick Beveridge Kennedy who joined the staff of the Agronomy Division, University of California, in January, 1914, moving into the newly completed Hilgard Hall on the Berkeley Campus. For over 15 years he carried out to the fullest the ideal set forth in stone carved letters over the front portal—"to rescue for human society the native values of rural life." Not least in importance among many practical accomplishments was his contribution to the knowledge of California grasses.

The contrasting characters of *Agrostis* and *Polypogon* may be summarized as follows:

Agrostis	*Polypogon*
(1) Glumes not awned (except Sect. *Microphyllae*).	(1) Glumes awned.
(2) Disarticulation above glumes (except *A. semiverticillata*).	(2) Disarticulation below glumes.

(3) Lemma awn if present often geniculate.	(3) Lemma awn never geniculate.
(4) Callus hairs common.	(4) Callus hairs never present.
(5) Lemma awn never terminal.	(5) Lemma awn terminal in Sect. *Polygonagrostis*.
(6) Palea often absent (always in Sect. *Microphyllae*).	(6) Palea well developed, from one-half as long as to subequal to lemma.

The awned-glumed species of *Agrostis* Sect. *Microphyllae* might fall into *Polypogon* on character (1), but fall short on the remainder and are better retained in *Agrostis*.

In the preparation of this paper material from the following herbaria has been examined: Agronomy Division Grass Herbarium, College of Agriculture, Univ. of California, Davis; Botany Department, Univ. of California, Berkeley; Dudley Herbarium, Stanford University; California Academy of Sciences; United States National Herbarium. In the interest of brevity the source of the specimens cited, except types, is not further specified.

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STUDIES IN THE SAPOTACEAE—IV. THE NORTH AMERICAN SPECIES OF MANILKARA

ARTHUR CRONQUIST

This paper completes the revision of the North American *Sapotaceae* which I have undertaken under the auspices of the Chicle Development Co. The work has been done under the direction of Mr. B. A. Krukoff, to whom I acknowledge my gratitude for various assistance. I wish also to thank the curators of the several herbaria who have kindly loaned specimens for study. These herbaria are abbreviated hereinafter as follows:

A—Arnold Arboretum, Harvard University, Jamaica Plain, Mass.
CR—Museo Nacional de Costa Rica, San José.
CU—Estacion Experimental Agronomica, Habana, Cuba.
F—Field Museum (Chicago Natural History Museum).
G—Gray Herbarium, Harvard University, Cambridge, Mass.
Mich—University of Michigan, Ann Arbor.
MO—Missouri Botanical Garden, St. Louis.
NY—New York Botanical Garden.
PR—Tropical Forest Herbarium, U. S. Forest Service, Rio Piedras, Puerto Rico.
US—United States National Herbarium, Washington, D. C.

The genus *Manilkara* was described by Adanson (Fam. Pl. **2**: 166. 1763), with a reference to an excellent figure in the pre-Linnaean *Hortus malabaricus*. It was generally reduced to *Mimusops* until revived by Dubard in 1915 (Ann. Col. Inst. Mart. III. **3**: 6–28). The first species assigned to it by Dubard was *M. kaukii* (*Mimusops kaukii* L.), and this has generally been considered to be the type. *Manilkara* is well separated from the strictly old-world *Mimusops* by its relatively long and lateral rather than small and basilateral seed-scar, and by having usually 6 sepals instead of 8, with attendant differences in number of corolla-lobes, stamens, and staminodes. Thirty-three species were recognized by Dubard, 13 of them in the new world.

Muriea, which has the staminodes replaced by functional stamens, has sometimes been considered distinct from *Manilkara*, but there seems to be no very good reason to believe that its two species, one Antillanean, the other Indian, are closely related. A new genus *Shaferodendron* has recently been segregated by Gilly (Trop. Woods **71**: 3–6. 1942), differing from *Manilkara* in its relatively long corolla-tube and short lobes, with the stamens inserted near the middle of the tube instead of at its summit. The difference seems to me of no more than sectional importance at best, especially since Gilly has shown that *Achras*, which sometimes has the corolla-tube longer than the lobes, must be submerged in *Manilkara*.

Achras is very similar to *Manilkara* in all significant features except the absence of the dorsal appendages of the corolla-lobes. Gilly has discovered transitional forms, previously identified as *Achras sapota*, in which the dorsal appendages are obviously present, but partly united with the corolla-lobes. Since the separation of the two genera depends solely on the technical character, Gilly's discovery of these transitional forms necessitates their union. As pointed out by Gilly (Trop. Woods **73**: 1–22. 1943), the original *Achras* L. is not the same as the group to which the name is now commonly applied, and cannot properly be used for it. The valid name for the genus under discussion is therefore *Manilkara*.

Inasmuch as I have found it necessary to reduce many previously proposed species, some discussion of specific concepts may be in order. My own is moderately conservative, based primarily on morphologic discontinuity, or very strong modal distribution. As in most tropical groups, the material now available for study is frequently insufficient to verify the existence of discontinuity, and I have in certain cases maintained, with appropriate comment, species which may have to be submerged when more material has been accumulated. The names which I have reduced without comment are those which I believe to be based on trivial and inconstant variations.

Our species of *Manilkara* are in general separated by strong floral characters, although they may be vegetatively very similar. Sterile specimens may be difficult or even impossible to determine with certainty, even after one is familiar with the entities involved, except as vegetatively similar species are eliminated by geographic considerations.

The "sapodilla-nispero complex" (species No. 9–12 of this treatment) has recently been revised by Gilly (loc. cit.), who segregated nine new species, based wholly on floral characters, from *Manilkara zapotilla* (*Achras sapota* of auth.). Four of these segregates are here referred back to *M. zapotilla;* the other five are grouped under two of their number, *M. staminodella* and *M. meridionalis*. I am reluctant to recognize specifically plants which are in the herbarium vegetatively apparently identical, but the floral variation within what has been called *Achras sapota* is so great as to demand some sort of segregation until it is conclusively shown that all the variants are parts of a single breeding population. It is interesting and perhaps significant that the sapodilla is divided by the chicleros into three varieties, but I have not been able to correlate these in the herbarium with the three apparent morphological species. (See Egler, Bull. Torrey Club **71**: 235–245. 1944.)

The names nispero and bullet-wood are applied more or less indiscriminately to most of the species. *M. zapotilla*, and its close relatives *M. staminodella* and *M. meridionalis*, are commonly known as sapodilla, but this name, alone or in various combinations or variations, is often used for other species as well. *M. emarginata*, for example, is known in Florida and the Bahamas as wild dilly. *M. bidentata* is often called balata, from its gum.

I have not considered it necessary to repeat all of the older and more obscure synonymy, much of which must in any case be taken to a certain extent on faith. This is available, for those who desire it, in Pierre and Urban's treatment of the *Sapotaceae* of the West Indies (Symb. Ant. **5**: 95–176. 1904), and in Gilly's revision of the *Manilkara sapodilla* group (Trop. Woods **73**: 1–22. 1942).

MANILKARA Adans.

Trees; leaves alternate, exstipulate; primary lateral veins parallel, straight or nearly so, but not especially crowded; reticulum evident (and close) or obscure; flowers perfect, or rarely unisexual; sepals biseriate, commonly 6, occasionally 8, or in one species sometimes 4; corolla-lobes as many as the sepals, each with a pair of dorsal more or less petaloid appendages at the base, or these partly or wholly fused to the lobes, or rarely vestigial; stamens as many as the corolla-lobes and opposite them, alternating with an equal number of staminodes (sometimes nearly obsolete), or these sometimes replaced by functional stamens; ovary about 6–14-loculate; ovules attached laterally; seed-scar relatively long, lateral; endosperm copious.

KEY TO THE SPECIES

1. Corolla-lobes and their appendages free nearly or quite to the summit of the tube.
   2. Stamens as many as the corolla-lobes and opposite them; staminodes alternate with the corolla-lobes, or obsolete.
      3. Corolla-tube not more than about half as long as the lobes, the stamens inserted at its summit; leaves various, but not narrowly oblong except in forms of *M. emarginata*. (*Eumanilkara*.)
         4. Appendages of the corolla-lobes about equaling or exceeding the proper lobes; staminodes various.
            5. Flowers about 3–10 in a cluster, small, the corolla about 5–7 mm. long; appendages, or some of them, bifid or trifid; fruit smooth or slightly roughened, scarcely mealy; Hispaniola to northern South America and Panama. 1. *M. bidentata.*
            5. Flowers about 1–2 in a cluster, large, the corolla about 9–14 mm. long; appendages entire; fruit mealy-roughened.
               6. Corolla-lobes and their appendages nearly or quite of the same texture; staminodes nearly as long as the corolla-lobes, about 5–9 mm. long; Puerto Rico and the Virgin Islands. 2. *M. pleeana.*
               6. Corolla-lobes conspicuously thinner and softer than their firm thick appendages; staminodes very short, about 1.5 mm. long; Jamaica. 3. *M. excisa.*
         4. Appendages of the corolla-lobes not more than about ¾ as long as the proper lobes; staminodes much shorter than the corolla-lobes.
            5. Staminodes petaloid, about 3.5–4 mm. long; leaves about 10–20 cm. long, the lower surface generally conspicuously paler than the upper and often rather yellowish; Costa Rica, Jamaica, and apparently Oriente, Cuba.
               6. Flowers about 1–3 in a cluster; staminodes broadly obovate to rhombic or ovate, irregularly laciniate-dentate; Costa Rica. 4. *M. spectabilis.*

6. Flowers about 4–6 in a cluster; staminodes lanceolate, entire; Jamaica, and apparently Oriente, Cuba. 5. *M. sideroxylon.*

5. Staminodes thickened, scarcely petaloid, up to about 1.5 mm. long, or obsolete; leaves about 4–10 cm. long, about the same color on both sides, or somewhat redder beneath; Florida; Bahamas; Cuba; Hispaniola. 6. *M. emarginata.*

3. Corolla-tube several times as long as the lobes, the stamens inserted near the middle; leaves narrowly oblong; Cuba. (*Shaferodendron.*) 7. *M. mayarensis.*

2. Stamens twice as many as the corolla-lobes; staminodes none; Cuba and Hispaniola. (*Muricа.*) 8. *M. albescens.*

1. Corolla-lobes and their appendages more or less united above the tube, or the appendages apparently wanting (two species, which may have only a short union of the lobes and their appendages, have the corolla-tube ⅔ as long to a little longer than the lobes, unlike any of the preceding species). (*Achras.*)

2. Flowers solitary in the axils; corolla-tube about ⅔–1⅓ as long as the lobes.

3. Corolla-lobes with evident dorsal appendages broader than and nearly or quite as long as the proper lobes.

4. Staminodes minute, scarcely or not at all petaloid, about 2 mm. long or less, less than half as long as the corolla-lobes. 9. *M. staminodella.*

4. Staminodes well developed, petaloid, about 2.5–6 mm. long, well over half as long as the corolla-lobes. 10. *M. meridionalis.*

3. Corolla-lobes entire or merely tridentate at the apex, the teeth all in about the same plane, the central one generally the largest. 11. *M. zapotilla.*

2. Flowers 2–5 in the axils; corolla-tube about ¼–½ as long as the lobes; appendages apparently wanting.

3. Leaves mostly 10–25 cm. long, 3–10 cm. wide, occasionally some of them smaller; continental. 12. *M. chicle.*

3. Leaves about 4–9 cm. long, 15–27 mm. wide; poorly known plant of Haiti. 13. *M. gonavensis.*

1. MANILKARA BIDENTATA (A. DC.) Chev. Rev. Bot. & Agr. **12**: 270. 1932.

Mimusops bidentata A. DC. Prodr. **8**: 204. 1844.
Mimusops sieberi A. DC. loc. cit.
Mimusops balata var. *domingensis* Pierre, Bull. Soc. Linn. Paris **64**: 508. 1885.
Mimusops riedleana Pierre ex Baill. Bull. Soc. Linn. Par. **2**: 922. 1891.
Mimusops balata var. *sieberi* Pierre, Symb. Ant. **5**: 166. 1904.
Mimusops nitida Urb. Symb. Ant. **5**: 167. 1904.
Manilkara riedleana Dubard, Ann. Col. Inst. Mars. III. **3**: 17. 1915.
Manilkara nitida Dubard, loc. cit., p. 18.
Mimusops darienensis Pitt. Contr. U. S. Nat. Herb. **18**: 249. 1917.
Manilkara darienensis Standl. Trop. Woods **31**: 45. 1932.

Large tree sometimes more than 20 m. tall; leaves mostly narrowly obovate, varying to elliptic, obtuse or broadly rounded to abruptly short-acuminate, about 6–30 cm. long and 3–12 cm. wide, glabrous from the first, or sometimes short-hairy when young, green or slightly reddish beneath, in herbarium specimens, the upper surface green or commonly darkened and somewhat purplish brown; petioles about 1.5–4 cm. long; flowers commonly about 3–10 in a cluster, the glabrous pedicels about 1.5–3 cm. long; sepals about 5–6 mm. long, the outer generally soon glabrate; corolla about 5–7 mm. long, the tube several times shorter than the narrow lobes; appendages about as long and nearly or quite as wide as the corolla-lobes, some or all of them deeply bifid or trifid, often irregularly so; staminodes about 1.5–3.0

mm. long; anthers about 1.8–2.5 mm. long; ovary glabrous, about 6–10-celled; style glabrous, about 4–5 mm. long; fruit globose or ellipsoid-globose, smooth or slightly roughened, but not mealy, about 2.5–3.5 cm. long.

TYPE: *Richard* s.n., French Guiana; photograph in Rev. Bot. & Agr. **12**: 269. 1932.

DISTRIBUTION: Hispaniola, Puerto Rico, Lesser Antilles, northern South America, and Panama.

HAITI: *Baker 7* (US); *Ekman H2580* (US). DOMINICAN REPUBLIC: *Abbott s.n.* (US), *196* (US); *Ekman 11184* (US), *15087* (US); *Taylor 6* (NY). PUERTO RICO: *Britton 8096* (NY, US), *8111* (NY), *Britton & Brown 6974* (NY); *Cowles s.n.*, (NY); *Gleason & Cook Q–14* (NY); *Heller 733* (NY); *Johnston 517* (NY); *Miller 1622* (US); *Sargent 204* (US); *Sintenis 1422* (MO, NY, US), *5174* (G, US), *6753* (MO, NY); *Stevens & Hess 2759* (NY); *Stevenson 1920* (NY, US). ST. JAN: *Britton & Shafer 574* (NY, US); *White 1497* (NY, US). TORTOLA: *Beard 318* (A); *Britton & Shafer 816* (NY, US); *Fishlock 471* (NY). GUADELOUPE: *Duss 3263* (F, MO, NY, US), *4125* (NY, US). DOMINICA: *Hodge 909* (G). MARTINIQUE: *Duss 252* (=*4557*) (F, G, MO, NY, US); *Hahn s.n.* (G). BARBADOS: *Eggers 7260* (A, US). PANAMA: Bocas del Toro: *Cox s.n.* (US). Panama: *Kluge 55* (US). CANAL ZONE: *Pittier 2699* (US), *4318* (G, NY, US), *4384* (US).

This species was long known as *Mimusops balata* (Aubl.) Pierre, or *Manilkara balata* (Aubl.) Dub., based on *Achras balata* Aubl. Aublet confused at least two old-world elements in his diagnosis, however, and it has been claimed (by Chevalier) that he did not even intend to include the native Guiana species to which the name has subsequently been applied. After detailed discussion, Chevalier concluded that the next available name, *Mimusops bidentata* A. DC., should be applied to the Guiana plant, and accordingly transferred it to *Manilkara*. He was followed in this treatment by Eyma (Rec. Trav. Bot. Neerl. **33**: 206–7. 1936), but it should be noted that Pierre, on much the same evidence, had earlier reached the opposite conclusion. In view of the fact that the application of Aublet's name is dubious, at best, I think it proper to adopt the next available name, which is *Manilkara bidentata* (A. DC.) Chev.

M. bidentata is common and widespread, but does not seem to be unusually variable, at least in North America, and I fail to understand the necessity for the various segregates which have been proposed.

2. **Manilkara pleeana** (Pierre) Cronquist, comb. nov.

Mimusops pleeana Pierre ex Baill. Bull. Soc. Linn. Par. 2: 923. 1891.
Achras duplicata Sessé & Moc. Fl. Mex. ed. 1. 92. 1894.
Mimusops duplicata Urb. Symb. Ant. 5: 169. 1904.
Manilkara duplicata Dub. Ann. Col. Inst. Mars. III. 3: 14. 1915.

Tree up to about 10 m. tall; leaves narrowly to broadly obovate, or elliptic, broadly rounded to abruptly acuminate at the apex, about 4–20 cm. long and 2–7 cm. wide, about the same color on both sides, or distinctly redder beneath, soon glabrous, borne on petioles about 6–28 mm. long; flowers 1 or 2 in the axils, the pedicels about 1.5–4.5 cm. long; sepals about 8–11 mm. long; corolla about 9–14 mm. long, the lobes several times longer than the tube, the appendages narrower than and about equaling the lobes;

staminodes petaloid, about 5–9 mm. long; anthers about 4–5 mm. long; ovary about 6–12-loculate, its style glabrous, 10–17 mm. long; fruit globose or depressed-globose, brown, mealy-roughened, about 3.5–7 cm. long.

TYPE: *Plée 237*, Puerto Rico, stated to be at the museum of Paris.

DISTRIBUTION: Puerto Rico, especially near the coast, and the Virgin Islands.

PUERTO RICO: *Britton 9775* (NY), *9807* (NY); *Britton & Brown 5907* (NY, US); *Britton & Cowell 1951* (NY, US); *Britton & Shafer 1545* (MO, NY, US), *1552* (NY); *Cowles 351* (NY); *Gleason & Cook B–17* (NY); *Gregory 442* (PR); *Holdridge 28* (NY, PR); *Shafer 2639* (NY, US); *Sintenis 3829* (G, MO, NY, US), *5767* (G), *6669* (G, MO, NY, US). TORTOLA: *Fishlock 92* (NY). ST. JAN: *Eggers s.n.* (March 8, 1877) (G, NY).

The date given for *Achras duplicata* Sessé & Moc. is taken from a notation in the New York Botanical Garden copy of the flora, by Dr. John Hendley Barnhart, bibliographer emeritus.

3. **Manilkara excisa** (Urb.) Gilly MS in herb., comb. nov.

Mimusops excisa Urb. Symb. Ant. 5: 459. 1908.

Tree sometimes 20 m. tall; leaves elliptic or elliptic-obovate, about 8–22 cm. long and 5.5–13 cm. wide, very firm, broadly obtuse to rounded or emarginate at the apex, glabrous, about the same color on both sides, or generally distinctly yellower beneath, borne on petioles about 2–4 cm. long; flowers 1 or 2 in the axils, the stout pedicels about 2–3 cm. long; sepals about 8–9 mm. long, thick and firm; corolla about 10 mm. long, the tube 3.5 mm. long, thick and firm; corolla-lobes thin, shorter than their thick and firm appendages; staminodes broad, thick, about 1.5 mm. long; anthers about 3.5–4.0 mm. long; ovary about 11-loculate, its style glabrous, 7 mm. long; fruit globose or depressed-globose, up to about 4 cm. long or perhaps more, brown, mealy-roughened.

TYPE: Not specified, from among *Sintenis 8765*, *8813*, and *8961*, all from near Troy, Jamaica. Since only No. *8961* is flowering, and the species is founded largely on floral characters, that number may well stand as the type (NY).

DISTRIBUTION: Known only from the type locality, near Troy, Jamaica.

JAMAICA: *Britton 586* (NY); *Sintenis 8765* (NY), *8813* (NY).

4. MANILKARA SPECTABILIS (Pitt.) Standl. Trop. Woods **31**: 45. 1932.

Mimusops spectabilis Pitt. Contr. U. S. Nat. Herb. 13: 465. 1912.

Similar to *M. sideroxylon*, sometimes 40 m. tall; flowers mostly 1–3 in the axils; sepals relatively broader, ovate or oblong-ovate; staminodes ovate to rhombic or obovate, erose-laciniate; ovary 10-celled.

TYPE: *Pittier 16012*, Puita, near Port Limon, Limon, Costa Rica, September, 1899 (G, NY, US).

DISTRIBUTION: Known only from the type collection, Limon, Costa Rica.

This species is very similar to *M. sideroxylon*, and may not be distinct. The available material of both species is inadequate, and, in view of their geographic separation, I am reluctant to combine them at this time.

5. MANILKARA SIDEROXYLON (Griseb.) Dubard, Ann. Col. Inst. Mars. III. **3**: 15. 1915.

Achras sideroxylon Hook. Rep. Par. Exh. 3: 61. 1856, hyponym.
Sapota sideroxylon Griseb. Fl. Br. W. Ind. 399. 1861.
Mimusops sideroxylon Pierre, Not. Bot. Sapot. 37. 1891.
Mimusops jamaicensis Pierre, Symb. Ant. 5: 176. 1904.

Tree up to nearly 25 m. tall; leaves rather narrowly elliptic or sometimes elliptic-oblanceolate, glabrous, or more or less white-sericeous-strigose beneath, about 10–20 cm. long and 3–7 cm. wide, broadly rounded to obtuse or acutish, the lower surface commonly paler than the upper, often yellowish; flowers mostly about 4–6 in a cluster, the pedicels 1–2 cm. long; sepals about 6–7 mm. long, lance-ovate; corolla about 8 mm. long, the tube half as long as the lobes, which evidently exceed their appendages; anthers about 3.5 mm. long; staminodes lanceolate, entire or nearly so, about 4 mm. long; ovary about 6–9-loculate, its style glabrous, about 6 mm. long; fruit brown, mealy-roughened, globose or ellipsoid-globose, about 2 cm. long.

TYPE: Grisebach mentions collections by *McNab* and *March*, in that order, from Jamaica.

DISTRIBUTION: Jamaica, and apparently Oriente, Cuba.

JAMAICA: *Britton 1644* (NY); *Harris 5379* (A, G, NY), *9845* (NY, US); *March s.n.* (G). CUBA: Oriente: *Ekman 16143* (NY, US).

Sterile specimens are distinguished only with difficulty from *M. zapotilla*, but have the leaves paler beneath, and without the loose rufous tomentum which generally persists for a time along the midrib of the latter.

6. MANILKARA EMARGINATA (L.) Britt. & Wils. Bot. Puerto Rico **6**: 366. 1926.

Large shrub or small tree commonly 4–10 m. tall; leaves short-petiolate, about 2–10 cm. long and 7–45 mm. wide, mostly 1.5–4 times as long as wide, elliptic or oblong, obtuse to more commonly broadly rounded or emarginate, rufous-pubescent beneath when young, generally soon glabrate, about the same color on both sides or distinctly redder beneath, the veiny reticulum evident or obscure; flowers about 1–3 in the axils, the pedicels about as long as the petioles, or longer; sepals about 4–10 mm. long; corolla about 4.5–10.5 mm. long, the lobes narrow, 2–4 times as long as the tube, the appendages about $\frac{1}{3}$–$\frac{2}{3}$ as long as the lobes; anthers about 1.8–3.9 mm. long; staminodes thickened, scarcely petaloid, up to about 1.5 mm. long, or nearly obsolete; ovary 6–12-loculate; style glabrous or more or less pubescent below; fruit obovate to spherical or depressed-globose, mealy-roughened, about 1.5–3.5 cm. thick.

TYPE: Description and figure in Catesby, Nat. Hist. Car. **2**: 87. 1733. Andros, Bahama Islands.

DISTRIBUTION: Southern Florida, Bahama Islands, Cuba, Hispaniola, and reputedly western Puerto Rico.

Four fairly well marked phases of this species may be recognized. Because of the paucity of flowering material of two of these, it seems unwise to attempt to construct a key. Except in parts of Oriente, Cuba, no more than one subspecies is known to occur in any given region.

6A. MANILKARA EMARGINATA (L.) Britt. & Wils. subsp. **typica** Cronquist, subsp. nov.

Sloanea emarginata L. Sp. Pl. 512. 1753, sensu stricto.
Mimusops parvifolia Radik. Sitzb. Akad. Wiss. München 12: 344. 1882.
Mimusops floridana Engl. Bot. Jahrb. 12: 524. 1890.
Mimusops sieberi, misapplied by auth. and in herbaria, not A.DC.

Leaves about 3–10 cm. long and 1.5–4.5 cm. wide, mostly 1.5–2.5 times as long as wide, borne on petioles about 5–25 mm. long; corolla about 6–10.5 mm. long, the tube about $\frac{1}{3}$–$\frac{1}{4}$ as long as the lobes; ovary consistently about 6-celled, its style glabrous or strigose-puberulent, about 6–13 mm. long. Florida and the Bahamas. An abundance of material of this subspecies has been available from Florida and the Bahama Islands. Since only one other species, *M. zapotilla*, occurs in the area, citations seem unnecessary.

6B. MANILKARA EMARGINATA (L.) Britt. & Wils. subsp. **wrightiana** (Pierre) Cronquist, comb. nov.

Mimusops wrightiana Pierre, Symb. Ant. 5: 171. 1904.
Mimusops grisebachii Pierre, loc. cit., p. 173.
Manilkara wrightiana Dubard, Ann. Col. Inst. Mars. III. 3: 16. 1915.
Manilkara grisebachii Dubard, loc. cit., p. 15.
Mimusops camagueyensis Urb. Rep. Sp. Nov. 24: 8. 1927.
Manilkara howardii Gilly, Trop. Woods 74: 15. 1943.

Similar to subsp. *typica*, but the ovary consistently about 9–12-celled, and the style commonly tomentose-puberulent toward the base. Habana to Camaguey and occasionally overlapping into Oriente, Cuba.

TYPE: *Wright 2917*, Cuba (G, MO).

CUBA: *Wright 2927* (G, MO). Habana: *Ekman 13580* (A, F, G, MO); *Leon & Roig 11516* (NY). Matanzas: *Acuña 4479* (CU); *Ekman 16515* (NY, US). Santa Clara: *Britton & Wilson 5662* (NY), *5723* (NY, US), *5748* (NY); *Cuesta 176* (NY); *Howard 5423* (G, NY); *Jack 5137* (A); *Ekman 19071* (F, US); *Leon 11594* (NY); *Roig 924* (NY); *Shafer 340* (NY, US), *421* (G, MO, NY), *2911* (NY). Oriente: *Ekman 4593*, Cauta River (US), *7449*, border of Camaguey (G, NY), *14952* (US); *Roig 5103*, Puerto Padre (CU).

6C. MANILKARA EMARGINATA (L.) Britt. & Wils. subsp. **jaimiqui** (Wright) Cronquist, comb. nov.

Mimusops jaimiqui Wright in Griseb. Cat. Pl. Cub. 64. 1866.
Manilkara jaimiqui Dubard, Ann. Col. Inst. Mars. III. 3: 16. 1915.

Leaves about 2–6 cm. long and 7–20 mm. wide, mostly 2.5–4 times as long as wide, or the smaller ones sometimes proportionately broader, borne on petioles about 4–10 mm. long; corolla about 5 mm. long, the tube $\frac{1}{3}$–$\frac{1}{4}$ as long as the lobes; ovary about 7–8-celled, its style mostly glabrous; limits of floral variation unknown. Isla de Pinos, Pinar del Rio, and Oriente, Cuba.

TYPE: *Wright 2918*, prope Chacco de Toro, western Cuba (G, MO, NY, US).

CUBA: *Van Hermann s.n.* (NY). Isla de Pinos: *Britton & Wilson 14362* (NY, US); *Ekman 12011* (US). Pinar del Rio: *Britton & Cowell 9997* (NY, US); *Britton & Gager 7016* (NY); *Ekman 11199* (F), *12688* (US), *12986* (NY), *17382* (NY); *Roig 6340* (CU); Oriente: *Ekman 4790* (G), *7600* (US), *9686* (G), *15890* (NY); *Roig 90* (NY), *6594* (CU).

6D. MANILKARA EMARGINATA (L.) Britt. & Wils. subsp. **haitensis** Cronquist, subsp. nov.

Leaves about 3–11.5 cm. long and 1–3.5 cm. wide, mostly 2–3 times as long as wide, borne on petioles up to 10 mm. long; corolla scarcely 5 mm. long, the tube about ½–⅓ as long as the lobes; ovary about 6–7-celled, its style puberulent below, about 4 mm. long; limits of floral variation not yet established. A subsp. *jaimiqui* differt foliis usque ad 11.5 cm. longis 3.5 cm. latis, tubo corollae pro rata longiore. Hispaniola.

TYPE: *Eyerdam 262*, Les Abricots, Gonave Island, Haiti, August, 1927 (NY); isotypes, G, US.

HAITI: *Ekman H2891* (US), *H8695* (US). DOMINICAN REPUBLIC: *Ekman 11326* (US), *15784* (US); *Holdridge 503* (PR).

Manilkara grisebachii, as represented by the type collection, has more tapering leaves and a slightly different aspect than subsp. *wrightiana*, and may eventually prove to be taxonomically separable.

It will be noted that subsp. *jaimiqui* is not known to occur in the intervening area between Oriente and Pinar del Rio, while subsp. *wrightiana* neatly fills the gap, also occasionally overlapping into Oriente. This peculiar distribution of subsp. *jaimiqui*, while interesting and unexplained, is not unique. *Bumelia conferta* is known from several collections in Oriente, and several in Pinar del Rio, but not between, and *Dipholis cubensis* likewise occurs in both Pinar del Rio and Oriente, without having been found in the other provinces. *Manilkara albescens* shows a similar disjunct distribution, but extends eastward from Pinar del Rio into Habana. In each of these cases, sufficient material has now been obtained to suggest that the apparent gap is a real one, and is not likely to be filled in by future collections.

The prominence of the close veiny reticulum, and the degree of reddishness, of the lower surfaces of the leaves, are variable in *M. emarginata*, and some segregates have been proposed on these bases, but the variation is continuous, and these characters are in my opinion quite without taxonomic significance in this instance.

7. **Manilkara mayarensis** (Ekm.) Cronquist, comb. nov.

Mimusops mayarensis Ekm. ex Urb. Symb. Ant. **9**: 418. 1925.
Shaferodendron mayarensis Gilly, Trop. Woods **71**: 4. 1942.
Shaferodendron moaensis Gilly, loc. cit.

Shrub or small tree up to 10 m. tall; leaves narrowly oblong, about 1–10 cm. long and 5–20 mm. wide, retuse, firm, scarcely or obscurely veiny, glabrous above, provided beneath with a very fine and close wax-impregnated rufous sericeous tomentum, which turns paler with age, the individual hairs often indiscernible under 25 diameters magnification; petioles about 2–12 mm. long; flowers solitary in the axils, on glabrous pedicels about 2–4 cm. long, 6-merous or sometimes only 4-merous throughout; sepals about 6–9 mm. long, the outer glabrous, the inner pulverulent; corolla about 9–11 mm. long, the lobes only about 1.5–2 mm. long, about equaling their dorsal appendages; filaments about 1 mm. long, attached near the middle of the corolla-

tube; anthers about 2.5–3 mm. long; staminodes linear-subulate or linear-lanceolate, about 1 mm. long, inserted at the level of the stamens or at the summit of the corolla-tube, or wanting; style about 10 mm. long; mature fruit unknown.

TYPE: *Ekman 9515*, in Sierre de Nipe ad Rio Piloto in carrascales, Oriente, Cuba.

DISTRIBUTION: Oriente, Cuba.

CUBA: Oriente: *Bucher 11103* (CU); *Ekman 15053* (NY, US); *Roig 1550* (CU, NY); *Shafer 4214* (NY, US), *8298* (NY, US).

Gilly's segregate, *Shaferodendron moaensis*, differs from the type in having the flowers 4-merous instead of 6-merous, but is otherwise very similar and probably represents a mere casual variant. Only a very few flowers of the species are available, so it is difficult to estimate the relative abundance of the 4-merous form.

The isotypes of *M. emarginata* subsp. *jaimiqui* at the Missouri Botanical Garden and the Gray Herbarium contain also pieces of *M. mayarensis*. If these latter specimens came from Pinar del Rio, as did the rest of the collection, the number of Sapotaceae known to occur in Oriente and Pinar del Rio, but apparently not in the intervening provinces, will be increased to five.

8. **Manilkara albescens** (Griseb.) Cronquist, comb. nov.

Bassia albescens Griseb. Cat. Pl. Cub. 164. 1866.
Mimusops albescens Hartog, Trim. Journ. Bot. 17: 358. 1879.
Muriea albescens Hartog ex Baill. Hist. Pl. 11: 269. 1891.
Mimusops azulensis Urb. Symb. Ant. 9: 418. 1925.
Muriea eyerdamii Gilly, Trop. Woods 71: 5. 1942.

Tree about 6–10 m. tall; leaves about 6–17 cm. long, 2.5–6 cm. wide, mostly elliptic or elliptic-oblong, broadly rounded to occasionally acute or even acuminate at the apex, provided beneath with a very fine and close somewhat waxy sericeous pubescence, which may be pallid, rufous, or so obscure as to escape observation under less than 25 diameters magnification; petioles about 6–30 mm. long; flowers about 2–8 in the axils or at defoliated nodes, the pedicels about 12–18 mm. long; sepals about 4–5 mm. long, all closely sericeous-tomentose; corolla about 6–6.5 mm. long, the tube $\frac{1}{3}$–$\frac{1}{2}$ as long as the lobes, the lateral appendages about equaling the lobes; stamens twice as many as the corolla lobes, all antheriferous, the anthers about 2 mm. long or less; staminodes absent; ovary about 6–10-loculate, its style about 3.5 mm. long; fruit globose, about 12–16 mm. thick, mostly 1–2-seeded; seeds about 10–12 mm. long, with a conspicuous cicatroid ventral flange.

TYPE: *Wright 2919*, western Cuba, near Retiro (G, NY, US).

DISTRIBUTION: Pinar del Rio, Habana, and Oriente, Cuba, and Hispaniola.

CUBA: *Cowles 1189* (NY). Pinar del Rio: *Britton 10006* (NY); *Ekman 12982* (NY); *Hermann 607* (CU); Habana: *Ekman 13707* (US). Oriente: *Ekman 15866* (NY), *4376* (US). HAITI: *Ekman 3363* (US), *H3347* (US), *H3317* (US); *Eyerdam 233* (G, NY, US). DOMINICAN REPUBLIC: *Ekman 12065* (US); *Scarff 18E* (F).

9. MANILKARA STAMINODELLA Gilly, Trop. Woods **73**: 10. 1943.

M. striata Gilly, loc. cit., p. 11.

Similar to *M. zapotilla;* leaves about 5–14 cm. long, 2.5–5 cm. wide; corolla-tube more or less pubescent, from about $\frac{3}{5}$ to fully as long as the lobes; corolla-lobes and their dorsal appendages subequal, united for about $\frac{1}{4}$ their length, the lobes oblanceolate or spatulate and narrower than their lanceolate or ovate appendages, but all of nearly the same texture; staminodes minute, about 1–2 mm. long, entire or bifid, scarcely or not at all petaloid, reflexed or sometimes erect; ovary about 6–9-loculate; fruit unknown.

TYPE: *Schipp 1310*, Camp 33, British Honduras-Guatemala survey, 2850 feet alt., April 29, 1934 (A, F, G, MO, NY).

DISTRIBUTION: British Honduras, and El Peten, Guatemala.

BRITISH HONDURAS: *Stevenson s.n.*, Chiquibul River, 1926 (US).

10. MANILKARA MERIDIONALIS Gilly, Trop. Woods **73**: 12. 1943.

M. meridionalis var. *meridionalis* Gilly, loc. cit., p. 13.
M. meridionalis var. *caribbensis* Gilly, loc. cit., p. 13.
M. tabogaensis Gilly, loc. cit., p. 10.
M. rojasii Gilly, loc. cit., p. 11.

Similar to *M. zapotilla;* leaves about 7–13 cm. long, 3.5 cm. wide; corolla-tube glabrous or pubescent, from about $\frac{2}{3}$ as long to a little longer than the lobes; corolla-lobes and their dorsal appendages subequal, or the appendages longer, united for about $\frac{1}{3}$–$\frac{2}{3}$ their length, the lobes oblanceolate or spatulate, generally narrower than their mostly lance-ovate to elliptic or obovate appendages, but all nearly of the same texture; staminodes well developed, petaloid, about 2.5–6 mm. long, more than half as long as the corolla-lobes; fruit brown, strongly mealy-roughened, ovoid or subglobose, up to 3.5 cm. long or perhaps more; seed-scar extending from near the base to well beyond the middle of the strongly compressed seed.

TYPE: *Biolley 17308*, Esparta, Punta Arenas, Costa Rica, February, 1909 (NY—photo, US).

DISTRIBUTION: Guerrero, Mexico, to Colombia and Venezuela; also, probably as an introduction, in Cuba and St. Croix, and perhaps elsewhere in the West Indies.

MEXICO: *Liebmann 304* (A). Guerrero: *Palmer 71*, Acapulco (A, G, MO). COSTA RICA: Punta Arenas: *Biolley 2023* (US). San José: *Rojas 524* (F, CR, MO, NY). PANAMA: *Hayes 793* (NY). Panama: *Standley 27099* (US); *Woodson, Allen & Seibert 1455* (A, MO, NY). CUBA: Pinar del Rio: *Britton & Cowell 9991* (G, NY, US). ST. CROIX: *Thompson 960* (NY).

11. MANILKARA ZAPOTILLA (Jacq.) Gilly, Trop. Woods **73**: 20. 1943.

Achras zapota of authors, not L. 1753.
Achras zapota β *zapotilla* Jacq. Stirp. Am. 57. *pl. 41.* 1763.
Achras zapotilla Nutt. N. Am. Sylva 3: 28. 1849.
Manilkara calderonii Gilly, Trop. Woods 73: 18. 1943.
M. conzattii Gilly, loc. cit.
M. gaumeri Gilly, loc. cit., p. 19.
M. breviloba Gilly, loc. cit., p. 19.

Large tree sometimes 40 m. tall; leaves clustered toward the ends of the twigs, elliptic or nearly so, rounded to acuminate at the apex, mostly 5–15

cm. long and 2–6 cm. wide, loosely rufous-tomentose beneath when young, soon glabrate, or more tardily so along the midrib, about the same color on both sides, borne on petioles about 1.5–3 cm. long; flowers solitary in the axils, the pedicels nearly as long as the petioles, or a little longer; sepals about 6–10 mm. long; corolla about 5–13 mm. long, the tube $\frac{2}{3}$–$1\frac{2}{3}$ as long as the lobes, glabrous or slightly hairy; corolla-lobes entire, irregularly toothed, or shallowly tridentate at the apex, the teeth all in about the same plane, the central one generally the largest; staminodes petaloid, about equaling the lobes; anthers about 1–3 mm. long; ovary about 9–12-loculate, densely short-hairy; fruit brown, mealy-roughened, ellipsoid, ovoid, or subglobose, variable in size, sometimes 10 cm. thick; seeds strongly compressed, commonly 16–23 mm. long and 8–16 mm. wide, the linear scar extending from near the base to beyond the middle, sometimes nearly to the top.

TYPE: Description and figure in Browne's Civil & Natural History of Jamaica, p. 200, pl. 19.

DISTRIBUTION: Widely distributed from southern Mexico to northern South America, and from southern Florida through the West Indies, but probably native only on the continent, from Mexico to Costa Rica.

A series of representative specimens has been cited by Gilly; further citation seems superfluous.

12. MANILKARA CHICLE (Pitt.) Gilly, Trop. Woods **73**: 14. 1943.

Achras chicle Pitt. Jour. Wash. Acad. Sci. **9**: 436. 1919.
Achras calcicola Pitt. loc. cit., p. 438.
Manilkara calcicola Gilly, Trop. Woods **73**: 15. 1943.
Manilkara calcicola var. *columbiana* Gilly, Trop. Woods **73**: 17. 1943.

Tree up to 40 m. tall; leaves oblanceolate or elliptic-oblanceolate to occasionally elliptic or narrowly obovate, mostly 10–25 cm. long and 3–10 cm. wide, some of them occasionally a little smaller, broadly rounded or obtuse to sometimes acuminate, usually conspicuously paler and more yellowish beneath than above, also very finely and closely sericeous-strigose beneath when young, but eventually glabrate; flowers about 2–5 in the axils, the pedicels about 15–30 mm. long; sepals about 5.5–9 mm. long, sericeous-tomentose; corolla about 4.5–8 mm. long, the tube $\frac{1}{4}$–$\frac{1}{2}$ as long as the lobes; dorsal appendages wanting; anthers about 3 mm. long; staminodes petaloid, erose, laciniate, or bifid, about 2.5–4.5 mm. long; from scarcely more than half as long to about as long as the corolla-lobes; ovary 6–10-loculate; fruit subglobose or obovoid, about 1.5–4 cm. long, brown and mealy roughened; seed-scar narrow and lateral, but scarcely extending to the middle of the strongly compressed seed.

TYPE: *Pittier 8537*, Vega Grande, near Los Amates, Izabal, Guatemala, May, 1919 (G, NY, US).

DISTRIBUTION: Oaxaca, Mexico, through Central America to Colombia.

MEXICO: Oaxaca: *Llewelyn Williams 9574* (A), *9432* (A, US). BRITISH HONDURAS: *Gentle 3186* (A, Mich, NY); *Lundell 689* (A, Mich); *Record 54* (US); *Schipp 1264* (A, G, Mich, MO, NY); *Walter s.n.* (April, 1915) (G, US). GUATEMALA: Izabal: *Whitford & Stadtmiller 75* (G, US). EL SALVADOR: *Calderon 320* (NY, US), *1371* (US), *2052* (US), *2215* (US). COSTA RICA: Guanacaste: *Cooper 10382* (US); *Standley & Valerio 45660* (US), *48582* (US), *48791* (US). CANAL ZONE: *Pittier 3457* (G, NY, US); *Standley 26384* (US). PANAMA: Darien: *Pittier 5698* (G, NY, US).

13. **Manilkara gonavensis** (Urb. & Ekm.) Gilly MS in herb., comb. nov.

Mimusops ? gonavensis Urb. & Ekm. Ark. Bot. **22A**(17): 76. 1929.

Large tree; leaves elliptic-oblanceolate, about 4–9 cm. long and 15–27 mm. wide, rounded or retuse at the apex, glabrous above, obscurely sericeous-strigose and sometimes reddish beneath, probably eventually glabrate; petioles about 7–20 mm. long; flowers about 4 in the axils, the pedicels 10–13 mm. long; sepals about 5 mm. long, the outer broader and firmer than the inner; corolla about 5.5 mm. long, the tube a little more than $\frac{1}{3}$ as long as the lobes; dorsal appendages apparently wanting; staminodes about as long as the corolla-lobes, but narrower; anthers about 2 mm. long; style about 3.5 mm. long; fruit unknown.

TYPE: *Ekman H8741*, base of Morne Fort-Couer, 200 m., Gonave Island, Haiti, July 29, 1927 (US).

DISTRIBUTION: Known only from the type collection, Gonave Island, Haiti.

Only fragmentary flowers of this species were available to Urban, and there is some doubt as to the proper interpretation of these, but they seem unquestionably manilkaroid. The isotype at US, the only specimen available to me, is sterile.

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THE EFFECT OF COLCHICINE AND ACENAPHTHENE IN COMBINATION WITH X-RAYS ON PLANT TISSUE—I. INTRODUCTION[1]

MICHAEL LEVINE[2]

Colchicine, the alkaloid extracted from the seed or corm of *Colchicum autumnale* L., the meadow saffron, has been known for many years. Houdé isolated this substance in 1887 as a yellow, flocculent material soluble in cold water, alcohol, and chloroform. When injected into the body in small doses, it produces gastrointestinal symptoms, such as vomiting and diarrhea, and in some respects behaves like muscarine, pilocarpine, physostigmine, and snake venom. The early uses of colchicine are given by Lits and his associates (1938a,b) to which the reader is referred.

Dustin (1934) investigated the action of colchicine on karyokinesis and cytokinesis in tumor tissue, and his papers resulted in the development of a number of lines of experimental study, effective in producing genetic changes in plants; the chromosome number in plants has been polyploidized and mutations have been produced at will. Colchicine has been used, furthermore, as a device to facilitate the study of the effects of hormones on various tissues of the animal body, and as an aid in cytological studies. It has stimulated interest in a search for other chemicals that affect the normal processes in nuclear and cell divisions and, finally, coupled with x-ray irradiation it has been used as a therapeutic agent in the treatment of cancer in man and the lower animals, and of bacterial overgrowths on plants.

These different phases of the colchicine literature have been reviewed (Levine 1945a,b), but the large number of reports on colchicine now extant make it impracticable to include all in a general survey. Hence only the salient features of the problem will be mentioned here, and emphasis given to those studies that deal with the effects of colchicine alone or in combination with x-rays on animal and plant hyperplasias.

The early studies on the effects of colchicine on cancer were fragmentary and without experimental basis. The belief that colchicine is an ameliorative in cancer seems to have been derived from some observations on gouty patients who were suffering concurrently from cancer. It was asserted that these patients showed improvement and that the cancerous condition was arrested after treatment with colchicine. Dixon and Malden (1908) were the first to

[1] This work will appear in three parts; a list of literature cited will be found in part III.

[2] Valuable assistance was rendered by Samuel Markowitz and Eleanor Acham, R.N.

study the pharmacological properties of colchicine on the blood and bone marrow of rabbits, rats, dogs, and in one or two instances of man. Rabbits injected subcutaneously with colchicine showed transient leucopenia, and a diminution in the polymorphonuclear cells. The administration of large doses of colchicine caused the appearance of abnormal cells, and normoblasts were commonly found. Bone marrow elements were observed in the general circulation and marrow smears showed an abundance of mitotic cell divisions.

The study of the mechanism of nuclear and cell division and attempts to alter their course have been in progress for many years. In 1933(a,b) Dustin and Grégoire studied the effects of various compounds on mitosis in mouse sarcoma 180. Dustin (1934) continued these studies using trypaflavine, rivanol, isamine blue, malachite green, arsenicals, benzol, iodine, zinc, mercury, thallium, and certain microbic toxins which he described as karyoklastic agents, and showed that colchicine has a stimulating effect on cell division much like that produced by sodium cacodylate. The number of nuclear divisions was calculated to be 15 times as great as that in untreated tumor tissue. These divisions were followed by karyorrhexis. Colchicine produced the maximum number of division stages in the sarcoma at the ninth hour after injection. Similar reactions were observed in the Kupffer cells, reticuloendothelial cells, the megocytes, and testicular cells.

Dustin (1937) studied further the effects of numerous substances on cell division and suggested they could be arranged in two classes: The first he characterized as having essentially an inhibiting effect on karyokinetic division that resulted in "karyoklastic shock." Substances in the cacodylate group he considered to be powerful excitants of mitotic division. He described the cytoplasm of these cells as turgescent; the prophase stages as of short duration, followed by atypical metaphase stages. The prolonged metaphase stage, which was characteristic of colchicine treatment, showed chromosomes condensed into compact masses, which he described as "radiomimetic." These mitoses either disintegrated, or were completed without the aid of spindle fibers. This division was frequently followed by the development of "monstrous" nuclei. Dustin believed that malignant cells are highly sensitive to this alkaloid. He (1938) showed, too, that the dosage of colchicine required to bring about extreme mitotic activity in tissues of the mouse was a very small fraction of that required for cacodylate. He found that the reaction occurred principally in the generative zone, or in cells made to divide by various means such as trauma, inflammation, carcinogenic activity, or hormones. Achromatic figures, asters, and spindles were totally lacking in these "colchicinized" cells. While some cells showed complete pycnosis, normal telophase stages and cytoses occurred. Some cells assumed normal telophase stages and formed giant or polyploid nuclei. Dustin proposed the name of "stathmocinesis" for this type of indirect division, and applied the name

"stathmocinetic poison" to colchicine. He contended that the arrest of nuclear division in the metaphase was preceded by a phase of excitation that distinguished this poison from those that merely inhibited division.

Effect of Colchicine on Plants. Havas (1937a), one of Dustin's collaborators, studied the effect of colchicine on plants inoculated with *Bacterium tumefaciens*, an organism that induces crown-gall. He observed that colchicine stimulated the appearance of tumors, but found when the end results were examined that tomato stems treated with colchicine bore tumors that were but half the weight of those in the controls. This led him to believe that colchicine is detrimental to the general development of the plant. Tomato crown-galls painted with a mixture of lanolin and colchicine were reduced in weight as compared with the controls. In *Pelargonium* stems there was no effect on the size of the tumor. *Begonia* stems, covered over a scarred area of about 1 cm. with a mixture of lanolin and colchicine, were stimulated to development in the area, while similar treatment of *Impatiens* proved toxic in some cases; the resistant stems, however, produced adventitious roots. Havas (1937b) studied further the effects of colchicine on germinating seeds and seedlings of a pure line of "Wilhelminia" wheat. Roots and root-hair development were stimulated at first, but the effects were followed by a depression of the growth rate and finally by complete arrest. Colchicine effects were shown in these seedlings by the development of bulbous hypertrophy of the root-tips and the liquefaction of certain parenchymatous elements. Havas (1938) later attempted to show that colchicine effects are of a hormonal nature, as evidenced by the appearance of adventitious roots, "pseudo-neoplasms" on root-tips, and hypertrophy of the coleoptile in seedlings, and the stimulation of somatic growth in *Begonia*.

Havas believed he was dealing with a "phytohormone" comparable with the wound hormone, traumatin, yet concluded that colchicine is not a hormone but a mobilizer of the hormone already present in the plant. The hypertrophies produced on root-tips he (1939) thought analogous to crown-gall disease.

The contention of Dustin and his associates that colchicine inhibits tumor growth resulted in many studies designed especially to determine this point. Animal pathologists directed their attention to its effects on a number of different types of neoplasia in man and the lower animals, but no other type of plant overgrowth commonly referred to by botanists as tumors, such as the potato wart, club root, and nematode galls, has so far been investigated.

Brown (1939), one of the first investigators associated with experimental production of crown-gall, made a series of investigations to determine the therapeutic effect of colchicine on these bacterial overgrowths. She attempted to prevent crown-gall as well as to destroy it when fully formed. Eight species of plants were under observation, Paris daisy, French marigold, four

o'clock, *Bryophyllum*, *Kalanchoë*, *Nicotiana glauca*, kidney bean, and tomato. Brown concluded that colchicine does not prevent formation of the overgrowths caused by *B. tumefaciens* or indoleacetic acid.

Additional attempts to kill or prevent further development of fully grown crown-galls led to the conclusion that death of the galls was not due to the direct killing or inhibiting action of colchicine on the bacterial organisms but that the colchicine affected the growth substances in the plant.

Brown (1942) further studied the effects of acenaphthene, methylnaphthalene, α-nitronaphthalene, 3,5-dibromopyridine, heptyl aldehyde and apiole. These substances were incorporated in a paste made of lanolin. Apiole induced dwarfing of the treated plant but no blackening of the tissue nor death; α-methylnaphthalene (50 per cent and 100 per cent) inhibited growth, heptyl aldehyde, as well as α-methylsalicylate used in full strength, caused death. The age of the tumor, Brown pointed out, affected the survival rate of the growth; young tumors were inhibited, old tumors were killed.

Dermen and Brown (1940a,b) studying the cytological effects of colchicine on plant tumors, found cellular changes associated with excessive polyploidy in the affected meristematic cells of the tumor. The effects induced by the colchicine were not immediate, for growth in controls and treated tumors continued for a week; then the treated tumors blackened and eventually died. The principal cytological change accompanying these morphological ones was multiploidy, which resulted in large nuclei in hypertrophied cells of the treated tissue. The size of the cells so produced had definite limits, the authors believed, beyond which death followed. Dermen and Brown suggested repeated colchicine injections in conjunction with irradiation as a therapeutic measure for cancer.

Solacolú, Constantinesco and Constantinesco (1939), who treated crown-galls on stems of *Pelargonium zonale* and *Ricinus communis* with colchicine, observed that a layer of meristem was formed between the tumor and the host; this new tissue became suberized and thus cut the metabolic exchange between plant and tumor so as to kill the new growth.

The effect of colchicine on animal itssue *in vivo* and *in vitro* has been reviewed by a number of workers and more recently by Levine (1945a,b). The reader is referred to these papers for details.

Colchicine and X-rays. Brues and Jackson (1937) studied the nuclear abnormalities induced by colchicine and other substances in a rat sarcoma, and suggested that the size of the dose determined the degree of aberrant cytological behavior. In a later paper, Brues, Marble and Jackson (1940) described the effects of the daily administration of colchicine on animal tumors and regenerating tissue. They believed that a narrow range of dosage exists that causes the characteristic effect upon cell division, and that this dosage can be injected daily without causing the death of the animal. The

belief that cells in mitosis are most susceptible to the effects of roentgen radiation led them to study the influence of x-rays on colchicinized tumors. Colchicine alone caused no regressions, though the tumors remained quiescent or retarded. As there was little difference between the tumors that were irradiated only and those given colchicine and irradiation, Brues and his associates concluded that colchicine has no effect on the response of these tumors to irradiation.

Guyer and Claus (1939), on the other hand, used 672 rats with Flexner-Jobling carcinoma in a series of experiments to test the combined effects of colchicine and x-rays on this tissue. They found that 0.1 mg. of colchicine per 100 g. of body weight administered subcutaneously coupled with irradiation of 3000r proved lethal to these animals in 2–3 weeks; 4500r given in three doses of 1500r each administered at intervals of two weeks or more were better tolerated, but smaller doses of 188r to 375r, frequently repeated, proved more effective than the larger doses. Guyer and Claus believed that a far greater lethal effect was produced in their experiments by the combined effects of colchicine and x-rays than by either one alone. In studying the combined effects of colchicine and x-rays on the Flexner-Jobling tumor *in vivo*, 91 rats were used. These were divided into 3 groups: 32 were treated with colchicine and x-rays, 29 with x-rays, and 30 with colchicine. The x-rays were given in doses of 188r twice weekly, beginning 16 days after implantation, when the tumors had attained a size of 1–1.5 cm., and 15 hours after the colchicine had been injected. At the end of 6 weeks in the group that received both x-rays and colchicine a large number of animals were healed; few deaths were recorded. Guyer and Claus concluded that x-rays are definitely more lethal to fragments of cancer tissue from colchicine-treated animals than to comparable pieces of untreated animals, as shown by the infrequency of takes after transplantation. When colchicine was administered to rats bearing actively growing tumors 15–18 hours before irradiation, x-rays retarded or completely inhibited tumor growth. Hirshfeld, Tennant and Oughterson (1940) studied the combined influence of colchicine and radiation on a transplantable mammary mouse carcinoma, and concluded that colchicine did not strikingly increase the destructive effects of x-rays, nor did it have any effect on the regression of spontaneous tumors in strain A mice.

Seed, Slaughter and Limarzi (1940) investigated the effect of colchicine combined with x-rays on advanced carcinomas in man. The 4 cases reported consisted of 2 breast adenocarcinomas, 1 rectal tumor, and one unclassified mass in the neck of a male. Two of the subjects died of colchicine poisoning and the others of their tumors.

Acenaphthene and Other Substances. The effect of trypaflavine, sodium cacodylate, and colchicine on pathological and normal tissues stimu-

lated interest in the search for other substances which would induce similar changes. Dustin, Lits, Brues, Brown, and others have studied a number of substances with this point in view. Schmuk (1938) and later in association with Gusseva (1939) showed that acenaphthene, like colchicine, could induce polyploidy. The assumption that a certain relationship existed between polyploidizing substances and the carcinogenes led Schmuk and Gusseva to test many of these substances. The carcinogenes were dissolved in ether and poured over filter paper. When the ether evaporated, grains of corn, wheat, and barley were placed on the paper and water was added for germination. Schmuk found that wheat and barley seeds were polyploidized by acenaphthene, acenaphthylene, chloracenaphthene, bromacenaphthene, α-chlornaphthalin, α-bromonaphthalene, α-iodonaphthalene, α-dibromobenzol, methylnaphthalaether, 3,5-dibromopyridin, ethylnaphthoat, α-nitronaphthalin. Germinating legume seeds did not become polyploid but were resistant to the effects of acenaphthene.

Kostoff (1938a) followed Schmuk with studies on germinating seeds of wheat, rye, oats, barley, maize, rice, *Festuca*, and *Lolium*. The seeds were covered with crystals of acenaphthene for 4–9 days. Legumes (*Vicia, Erodium, Lothyrus, Medicago*) reacted slowly after an exposure of 6–12 days, while *Compositae* responded in 4–8 days. Kostoff showed that mitoses proceeded abnormally, forming polyploid nuclei. The chromosomes were spread in the cytoplasm, frequently giving rise to multinucleate cells. Floral buds of nine species of *Nicotiana* treated with crystals of acenaphthene produced abnormal microspores and abortive pollen grains. The viable pollen grains had unequal numbers of chromosomes. Kostoff (1938b) induced chromosome doubling in species of *Triticum* and *Secale* by subjecting the seeds to a saturated solution of acenaphthene with excess of crystals. He pointed out that long exposures to large amounts of sublimated particles of acenaphthene may injure or even kill plant tissues. Nebel's (1938) results with saturated solutions of acenaphthene on *Tradescantia* gave no polyploidy. Acenaphthene, it must be remembered, is only very slightly soluble in water and the sublimated crystals, it seems, alone produce the reactions. Kostoff (1938c,d) later concluded that colchicine was toxic while acenaphthene did not appear to be. In a later report, Kostoff (1939) induced polyploidy in some series of cereals by subjecting them to pulp from disintegrating corms of *Colchicum autumnale*, which suggested the possibility of finding polyploid plants among the species growing in nature in association with *Colchicum*. Bates (1939) tested this theory and found that other plants growing among corms of the meadow saffron revealed no abnormalities. In nature, Bates believes the polyploid individuals are suppressed in competition with the normal seedlings or established vegetables.

Gavaudan, Gavaudan and Durand (1938) tested acenaphthene on ger-

minating wheat seedlings. They found themselves in accord with Kostoff in that acenaphthene prevents spindle formation. These investigators also tested the efficacy of diphenyl and naphthalene and their derivatives on dividing cells. While arrested mitoses were observed, some of the derivatives like diphenylmethane were toxic, Gavaudan (1941) tested (1,2,3,4,5-tetramethylbenzene) durene and found that it induced mitotic inhibition similar to acenaphthene. Gavaudan and Gavaudan (1939b) discovered that apiole inhibited cell division. They found that *Hordeum* seedlings were very susceptible to apiole and showed tetraploid and octoploid cells after the first 24 hours. After colchicine, the authors believed, apiole was the second known substance existing in a natural state capable of modifying nuclear and cell divisions and capable of inducing polyploidy.

Simonet and Guinochet (1939a) reported the production of polyploidy in flax seedlings by paradichlorobenzene. This substance produced morphological changes similar to those effected by colchicine and acenaphthene. Simonet and Igolen (1940) investigated the vapor of the oil of leaves of *Citrus nobilis* on flax and on barley seedlings. The roots of the latter were more sensitive than the flax and marked disturbances of cell and nuclear divisions were observed. Such stages as the anaphase and telophase were lacking and the cells became multinucleate. Methylester of methylanthraml acid, the principal constituent of the oil of *C. nobilis*, produces similar reactions. Simonet and Guinochet (1939b) obtained effects with α-chloronaphthalene and α-bromonaphthalene which they believed comparable to those induced by colchicine. Simonet (1940) also claimed to have produced colchicine-like anomalies with 1,3,5-trinitro-m-xylene when barley and flax seedlings were tested. Shimamura (1939b) used sublimated acenaphthene on young flower buds of *Fritillaria* and observed abnormal nuclear division in pollen mother-cells. The pollen mother-cells divided into many cells, each containing small nuclei. Hukusima (1939) reported the production of polyploids in *Brassica alboglabra* with the aid of acenaphthene. The flowers were encased in small glass tubes, the walls of which were covered with crystals of acenaphthene. Favorski (1939) listed 12 chemicals among which were aurantia, tribromoaniline, α- and β-naphthylamine, trinitrophenol, and tribromophenol, that induced mitotic changes similar to colchicine. Garrigues (1939) compared the effects of chloral and colchicine on the roots of *Vicia faba*. Chloral, he reported, did not induce swellings of the root but changed the structure of the resting nucleus. Chloral affected cells above the meristem interfering with the cells in the elongation zone. De Mol (1939) applied acenaphthene in paste form mixed with formalin, alcohol, or water to roots of gladiolus. The colchicine-formalin paste killed the roots, while the alcohol mixture injured them. De Mol concluded that acenaphthene is less effective than colchicine. Weichsel (1940) used auramin on *Vicia faba* and barley, and acenaphthene on *Soya*, luzerne, and corn. She reported changes similar

to those obtained by Schmuk and Kostoff on the grass seedlings with bromonaphthalene and bromoacenaphthalene. Fatalizade (1939), too, showed that crystals of acenaphthene acted on F_1 seedlings of the cross *N. rustica* × *N. paniculata* and produced polyploids.

Colchicine in Cytology. Many of the reports on the growth effects induced by colchicine are accompanied by cytological studies of the germ as well as the somatic cells. Many investigations on colchicine deal with the cytological changes per se. Dermen (1940) reviewed the literature on polyploidy as induced by colchicine and gave an adequate summary of the technique employed in the production of these aberrant chromosomal behaviors in plants and animals. Wellensiek (1939) gave a short digest of the use of colchicine in polyploidy as well as an historical account of the properties of the alkaloid. Györffy (1940a,b) studied the chromosome numbers of polyploids obtained by colchicine treatment. He also summarized the results obtained with colchicine treatment up to 1940. Here only those reports which have a bearing on the problem described below will be mentioned.

Nebel (1937) and Nebel and Ruttle (1938) studied the nuclear changes in the stamen hairs of *Tradescantia*. Gavaudan and Gavaudan (1937) treated plants with colchicine and reported the arrest of growth of plants with 0.001–0.005 per cent solution. They observed an increase in chromosome number. In a later paper (1938) they noted that the limit of increase in the number of chromosomes was determined only by the difficulties of nutrition. This they believed could be surmounted by cultivating plantules or polyploid cells in tissue culture. Gavaudan (1938) studied seedlings of *Vicia faba* which were immersed for two hours for three successive days in a 1 : 1000 solution of colchicine. These plants grew slowly and showed diverse monstrosities of stomata and leaf structures. Tetraploid and even octoploid cells with numerous nucleoli were observed. These changes were associated with interference with the normal karyokinetic process.

The roots of *Allium cepa* were studied by Gavaudan, Gavaudan and Pomriaskinsky-Kobozieff (1937) as affected by colchicine. They found that 0.1 g. to 0.2 g. of colchicine per 1000 ml. in water induced bulbous hypertrophies behind the meristem of the root-tips. They reported large numbers of abnormal mitotic figures 40 hours after treatment. Pseudoanaphase stages were noted in which the chromosomes were vaguely arranged in a quadrilateral form (pseudotelophases) with the two chromosal groups united by a bridge of chromosomal material.

Eigsti (1938, 1940a) using the smear method studied the effects of colchicine on the roots of the onion, and of radish and corn seedlings. He found that the cytological changes were determined by the concentration of the colchicine solution, the time of exposure, and the activity of the embryonic cells at the time of treatment. Eigsti (1940b) believes that chromosome breakage is higher in colchicine-treated material than in the untreated cells

of the same species. This, he infers, induces variation other than polyploid changes.

Levan (1938, 1939) made studies on the cytological effect of colchicine in mitoses of roots of *Allium fistulosum* and *A. cepa*. Levan, too, observed that the treated roots ceased to elongate, but formed swellings at the root-tip meristem which he described as tumors. The volume of the meristematic cells increases but no new cells are formed. Levan showed that the cells in treated roots transferred to water reverted to normal mitosis. In colchicinized onion root-tips, he counted 128 and 256 chromosomes. Concentration as low as 0.0055 per cent colchicine caused disturbance of the spindle. The threshold value of colchicine on root mitoses of *A. cepa*, Levan believed, was reached with a 0.005–0.01 per cent solution after an exposure of four hours. Nebel (1937) found a 0.004 per cent solution of colchicine effective in plants, while Ludford (1936) showed that a solution of 0.00001 per cent is effective in animal tissue. Mangenot (1938a,b, 1939) studied the roots of onion (*Allium cepa*) and hyacinth (*Hyacinthus orientalis*), and of the seeds of lupine (*Lupinus albus*) grown in Knopf's solution to which 1 : 2000–1 : 3000 colchicine was added. He found that the roots remained alive after a long period in the mixture. He observed the *tumefaciens* effects of colchicine and ascribed this to a defect in the growth of the roots. The number of prophase stages was studied by Mangenot, who contended that the number of cells in this stage did not vary up to 102 hours of exposure to colchicine, after which it decreased slowly, while the number of metaphases, anaphases, and telophases fell off rapidly to zero. Levine and Gelber (1943) showed that with a colchicine concentration of 0.01 per cent, the maximum number of metaphase stages in the root-tips of *Allium cepa* was reached after an exposure of 24 hours. Continued exposure to the same solution caused a general reduction in the number of metaphases until the number reached in the 140th hour was smaller than that found in normal root-tips.

Shimamura (1939a) investigated the effects of the alkaloid, colchicine on the roots and seedlings of *Allium cepa*, *Lycopersicum esculentum*, and *L. pimpinellifolium*. He exposed the roots of the onion to a 0.4 per cent solution for two hours, after which they were placed in running water for one hour, and then fixed at varying intervals. Shimamura described in detail the chromosome behavior in the colchicine-treated onion root-tips. He believed that colchicine interfered with the mechanism that pulls the chromatids apart. In the absence of the spindle fibers Shimamura described an orientation of the chromosome material about a degenerate spindle substance. The tomato seedlings treated with colchicine produced tetraploid and myxoploid plants. In the roots of these seedlings aneuploidy was seen. Duhamet (1939) attempted to establish the colchicine concentration which would be most capable of producing a reaction in the roots of the white lupine grown *in vitro* and attempted to induce a diminution or suppression of these effects.

He observed that colchicine in concentration 10^{-4} inhibited completely growth of isolated roots in 10–12 days. The addition of heteroauxine in concentration 10^{-12} to this solution of colchicine interfered with the growth block induced by colchicine and was followed by a return to normal division. Levine and Lein (1941) studied the effects of various growth substances, such as vitamin B_1, indoleacetic acid, and colchicine on the number and length of roots of *Allium cepa* grown in water in which these substances were used singly or in combination. Colchicine in 10^{-3} solution inhibited root growth; when followed by exposure to a 10^{-8} solution of indoleacetic acid, stimulation of both the formation of new roots and the linear growth of roots occurred.

Irradiation with X-rays. It has been now generally conceded that x-rays and the beta and gamma rays of radium are valuable adjuncts to surgery if not self-sufficient agents in the effective treatment of neoplastic diseases of man. Many roentgenologists believe that the efficacy of these rays lies in their destructive action on chromosomes. The resting stages have been considered resistant. However, there are two principal groups of investigators whose studies primarily dealt with these highly important problems. Strangeways and his associates Oakly and Hopwood observed that irradiated tissue culture showed a decrease in the number of dividing cells. They observed that this decrease was due temporarily to an inhibition of the onset of mitoses. These views were supported by Kemp and Juel. On the other hand, Mottram, Richards, Grasnich, Holthusen, Alberti and Politzer and many others contended that cells are most sensitive to irradiation while in the process of mitosis. Love's (1931) studies on choroid and sclerotic tissues of embryo chicks of 8–9 days attempt to analyze the effects of x-rays on dividing cells. He studied the percentage of survival of dividing cells immediately after irradiation. He concludes that the reduction in the number of cells in mitosis after irradiation is due to an inhibition of some factor of those cells which normally would have entered mitosis during the period of irradiation. He states that the radio-sensitivity of a cell is a function of its displacement from maturity. When the displacement of a cell from its maturity is less than 100 minutes, the radio-sensitivity is constant and independent of displacement. When the displacement of a cell from its maturity is greater than three hours, its radio-sensitivity decreases. Studies on the effects of irradiation on chromosomes of animals and plants are too numerous to be included here. The recent literature dealing with the application of irradiation to onion root-tips is briefly outlined below.

Nichols (1941), working with Sax, investigated the chromosomes of non-irradiated root-tips of onion seedlings. He reports that chromosome aberrations are frequent in very young seedlings, while in older ones few chromosome abnormalities are found. Nichols believes that cells with chromosome aberrations are eliminated by differential survival of the normal and ab-

normal cells. Marshak and Hudson (1937) used the onion seedling root-tips as a biological method of measuring roentgen ray dosage. They believe that the biological response per roentgen (r) is independent of wave length over the region studied. They used small doses, 40–346r. Marquardt (1938) studied the effects of soft rays on root-tips of *Scilla campanulata* and on pollen mitosis in *Bellevalia romana*. He describes two kinds of effects which he calls primary and secondary. The first effect occurs in such nuclei as are found, at the time of irradiation, in mitosis or about to enter that state. The primary effects are described as clumping and fragmentation of chromosomes, lack of spindle formation, and indefiniteness of division polarity. The period following the primary effects is a mitosis-free interim after which the secondary effects become apparent. In the pollen studies there was no mitosis-free interim. The secondary effects bring about chromosome injuries, fragmentations and restitution processes, lateral chromatid translocations, ring-forming injuries, and inversion forms. Villars (1940) studied the effects of x-irradiation on colchicine-treated roots of seedlings of *Pisum sativum* and *Allium cepa*. These were placed in a solution of 1 : 2000 colchicine and irradiated after 40, 48, 96, and 120 hours of immersion. Their treatment had no effect on stages up to and including the prophase. In the following stage, the chromosomes agglutinated and fused into one mass, and spindle formation was inhibited.

Sax (1941) studied the effects of x-irradiation on the roots of *Allium cepa*. While the primary purpose was to describe the chromosomal changes induced by the x-rays, an exposure to 0.1 per cent colchicine for 24 hours was applied to facilitate this study. Aberration frequency was based on the number of chromosomal abnormalities per 100 cells counted. Sax describes primary and secondary effects produced by x-rays which are in accord with Marquardt's observations. Sax does not differentiate between the effects induced by colchicine and those by x-rays. He shows that high x-ray doses suppress nuclear division for from one to two days while low x-ray doses retard nuclear activity and the chromosome clumping persists for several days. The primary effects are evident on the metaphases, while the secondary effect involves the production of chromosomal aberrations which consist of chromosome breaks, usually followed by chromosome union to produce rings, dicentrics, inversion, translocations, and interstitial deletions. The secondary x-ray effects, Sax believes, persist for several cell generations, but are soon eliminated and cells with normal or balanced genoms survive. Sax used doses of x-rays from 150r to 600r. Larger doses, such as 1500–5000r, were used on seedlings of ornamental plants; the highest dosage killed or retarded the seedlings of most species studied.

The Function of Colchicine in Tumor Therapy. It has been shown that colchicine administered or applied in small doses to animals or plants has a retarding effect on mitosis in the cells of either growing vegetative or

germinal tissue. In animals, the metaphases begin to accumulate 2–3 hours after the colchicine is given, reach a maximum number in 10–15 hours, and then gradually return to normal. In cold-blooded species, the accumulation of these mitotic figures is much slower, and lasts 5–7 days. In the roots of onions the metaphases reach a maximum number at 24 hours and then slowly decline, in spite of the continued application of the drug, to a stage where the divisions are fewer than in normal, untreated roots. The reconstructed nuclei after the treatment frequently form polyploid giant cells which persist or are eliminated.

In malignant animal growths colchicine emphasizes the division phase. Many of the chromosomal aberrations found in malignant cells (Levine 1931) are analogous to those induced by colchicine. The evidence that colchicine increases these stages in the tumor cell cycle has been well established. The young peripheral cells, apparently diploid, become arrested in division and present hyperchromatic stages typical of the older parts of the tumor. These considerations suggest the use of colchicine in cancer therapy. However, some cells in the animal tumors return to the status of young active cells, which leaves the tumor capable of continued growth. The attempt to destroy these cells by additional colchicine raises the colchicine level to the lethal point and so causes death of the animal.

The application of x-rays to tumor tissue after treatment with colchicine seems to be indicated. The colchicine keeps the active peripheral cells of a tumor in the metaphase stage so that a much larger number of cells in division, a vulnerable stage, are exposed to the lethal effect of x-rays.

The results so far presented, however, have been inconclusive. Some investigators have found that colchicine alone causes complete regression of lymphoid tumors; others have seen some improvements in animals with carcinomas or sarcomas after colchicine and x-rays combined over comparable neoplasms treated only with x-rays.

Tumors induced on plants by bacteria or chemical means were destroyed by colchicine alone. The self-limiting nature of these tumor-like growths, however, precludes any comparison between the effects of colchicine on animal tumors and on the crown-gall disease of plants. However, in some cases, the plant overgrowths appear to die sooner after colchicine treatment than when left to complete their life cycle.

It thus appears that a study of the combined effects of colchicine and x-rays on a simple fundamental tissue, meristematic in nature and responsive to both agents, would simplify the interpretation of the results obtained from them. It was believed that such a study would serve as a forerunner of an investigation on the effects of these agents on animal tumors of a cytogenetic homogeneity.

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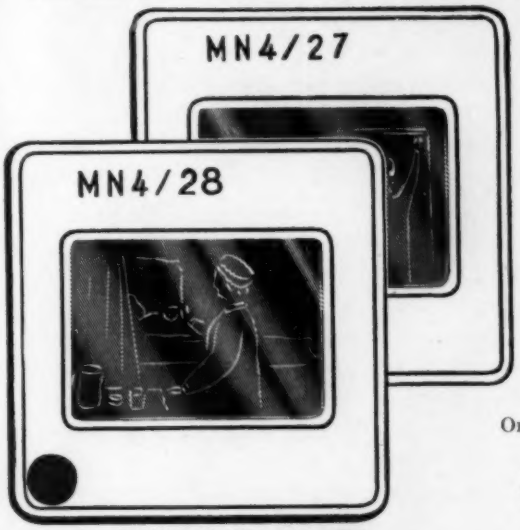

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